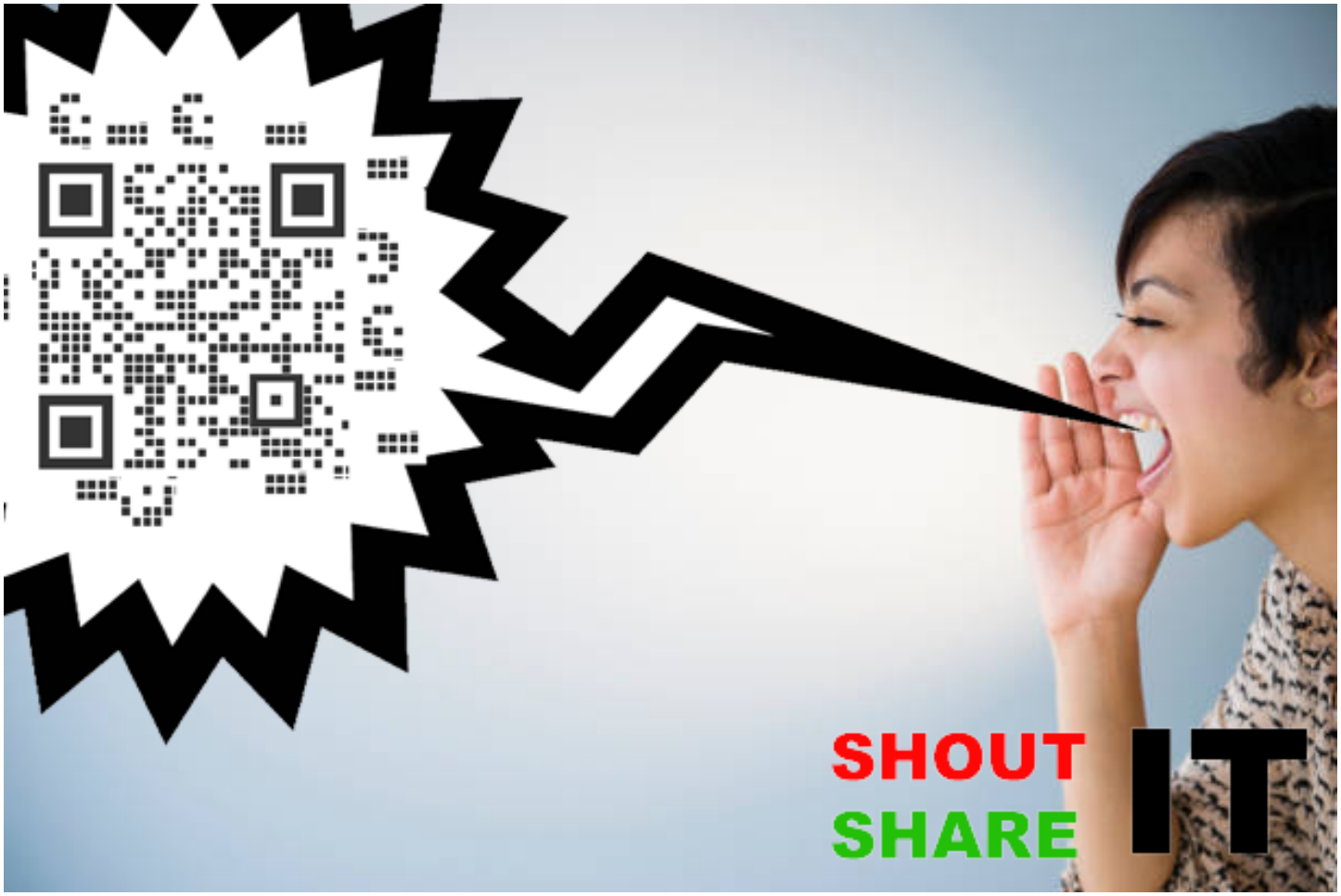
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STUDIES ON NORTH AMERICAN POLYSTOMIDAE, ASPIDOGASTRIDAE, AND PARAMPHISTOMIDAE

WITH ELEVEN PLATES

BY

HORACE WESLEY STUNKARD

Contributions from the
Zoological Laboratory of the University of Illinois under
the direction of Henry B. Ward. No. 84

THESIS

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INTRODUCTION

The knowledge of the trematodes of North America is very scanty. Information at hand consists largely of brief and scattered papers and comprehensive studies on the morphology of the larger groups are wanting. Such studies are needed as contributions to the knowledge of adult forms, and it is apparent also that knowledge of the anatomy and taxonomy of the adult is demanded in the solution of life history problems.

This paper contains the results of a study on the structure and classification of North American representatives of the families Polystomidae, Aspidogastridae, and Paramphistomidae. Because of certain structural and developmental features these three families are of particular interest and importance not only in the taxonomy but also in the phylogeny of the trematodes. The Polystomidae differ from all other known Heterocotylea in that they are endoparasitic; the Aspidogastridae are both ectoparasitic and endoparasitic, develop both directly and by means of an intermediate host, and in the adult condition are parasites of both vertebrates and molluscs; while the Paramphistomidae are the only forms retaining a primitive posterior sucker. These facts are significant and it is probable that further study into the structure and life history of these forms will throw considerable light on the general problems of development and taxonomy of the trematodes.

During the past three years the writer has made parasitological examinations of over three hundred North American fresh-water turtles. These comprise sixteen species collected from widely scattered localities. For assistance in securing this material, grateful acknowledgments are due Dr. N. A. Cobb of Washington, D. C., Professor A. W. Orcutt of Denison University, Professor W. E. Burge of the University of Illinois, Professor J. E. Ackert of Kansas State Agricultural College, and Professor W. W. Cort of Macalester College. The material of *Alassostoma parvum* was collected and turned over to me by Mr. T. B. Magath. A type specimen of *Polystoma coronatum* Leidy from the U. S. National Museum was placed at my disposal for study. The work was begun at the suggestion of Professor Henry B. Ward and carried on under his direction. Part of the material used in the investigation came from his private collection, and for this material as well as for criticisms and suggestions in the course of the work the writer wishes to express his appreciation.

All the forms described in this paper were studied as toto mounts; where sufficient material was available sections were made, and many were studied alive. The importance of the study of the living specimens can not be overemphasized as the best method of tracing the excretory system. Also, by observing the living animal as it moves, it is possible to measure the extent of normal variation in form that occurs in a single specimen as different shapes are assumed concomitant with the movements of the animal; in forms with such soft bodies and variable shapes, a study of preserved material alone has in many cases given false conceptions concerning morphological relationships of organs and systems. In toto mounts a support under the coverglass is necessary to prevent it from flattening and distorting the normal shape of the aspidogastrids and to avoid crushing the caudal disc of the polystomes. For the staining of specimens to be mounted in toto, better results were obtained by the use of carmine than by hematoxylin stains. For staining sections the method that proved most valuable was to use the hematoxylin stains for differentiating the nuclear elements and various plasma stains for counterstaining.

POLYSTOMIDAE

HISTORICAL REVIEW OF THE FAMILY

In 1758 Roesel von Rosenhof described and figured a "leech" from the urinary bladder of the frog. This is regarded as identical with the well known European parasite of the urinary bladder of the frog, described by Fröhlich (1791) as *Linguatula integerrimum*. M. Braun (1792) described *Planaria uncinulata* from the urinary bladder of the green water-frog and his description is so specific that there can be no doubt that he had the same form described by Fröhlich the previous year. Zeder (1800) founded the genus Polystoma to contain the three species, *Linguatula integerrimum* Fröhlich which he rechristened *Polystoma ranae*, *P. serratum*, and *P. pinguicola*. According to Stiles and Hassall (1908) the type was clearly intended to be *P. ranae* = *Planaria uncinulata*, and altho Braun had described the form correctly with the suckers and hooks at the posterior end of the body, Zeder erroneously stated in his characterization of the genus that the suckers were at the anterior end. *P. serratum* had been designated by Fröhlich (1789) as type of the genus Linguatula and *P. pinguicola* had been designated by Treutler (1793) as type of the genus Hexathyridium. That Zeder was in error in including these species in the genus Polystoma was demonstrated by later studies. However Rudolphi (1809) retained them in the genus Polystoma and listed three other species: *P. taenoides* Rud., *P. denticulatum*, Rud., and *P. venarum* (Treutler 1793) Zeder 1803. Among these species, it is probable that Treutler's description was of an artifact rather than a parasite, and the other two have been removed to the Linguatulidae.

Polystoma thynii was described from the gills of *Scomber thynnus* by Delaroche (1811). Rudolphi (1819) renamed this species *P. duplicatum* and added a new species *P. ocellatum* from the throat of *Emys europa*. This species is regarded as identical with that described by Kuhl and Hassalt (1822) from the nasal cavity of *Halichelys atra*. *P. logiginis* was described by delle Chiaje (1823) from *Loligo vulgaris*. Blainville (1828) oriented the polystomes correctly and transferred *P. integerrimum*, *P. ocellatum*, and *P. thynii* to a new genus Hexacotyle, naming *H. thynii* as type. According to the rules of zoological nomenclature, however, the genus Polystoma must be retained. Kuhn (1829)

described *P. appendiculatum* from *Squalus catulus*. Dujardin (1845) transferred *Diclibothrium crassicaudatum* Leuck. 1835 = *Diplobothrium armatum* Leuck. 1842 to the genus Polystoma, and listed as additional species, *P. duplicatum, P. pinguicola, P. ocellatum, P. integerrimum,* and *P. appendiculatum*. Diesing (1850) named *P. loliginis* and *P. appendiculatum* as types of new genera Solenocotyle and Onchocotyle. He removed *P. armatum* to the genus Diclibothrium Leuck. and retained in the genus Polystoma only the species *P. integerrimum* and *P. ocellatum*.

The genus Polystoma together with the genera Tetrastomum, Gryporhynchus, Hexathyridium, Notocotyle, Aspidocotyle, and Aspidogaster were included by the same author in the tribe Polycotylea.

In his revision Diesing (1859) reduced the trematodes to the rank of a tribe and divided the group into three subtribes: Acotylea, Cotylophora, and Plectanophora. The second of these subtribes he subdivided into three families: Monocotylea, Tricotylea, and Polycotylea. The last of these corresponds almost identically with his former tribe Polycotylea. He rejected Gryporhynchus, and added the genera Ancyrocephalus, Plagiopeltis, Heptastomum, Onchocotyle, Cyclocotyle, and Solenocotyle. In the family Polycotylea he recognized two subfamilies: Aplacocotylea with the suckers set directly in the body, and Placocotylea with the suckers set in a median posterior plate. In the latter he included the genera Onchocotyle, Polystoma, Cyclocotyle, Aspidocotyle, Aspidogaster, and Solenocotyle.

Then followed the great work of van Beneden (1858) with an experimental demonstration of the "direct" development of the many-suckered ectoparasitic trematodes, and the "indirect" development of the distomes. For these two groups he proposed the names Monogenea and Digenea. In the former he recognized two families: the Tristomidae with a single posterior sucker, and the Polystomidae with several posterior suckers. In the Polystomidae he included the genera Polystoma, Diplozoon, Octobothrium, Axine, Onchocotyle, Calceostoma, and Gyrodactylus.

Later van Beneden and Hesse (1863) made the genera Octocotyle (= Octobothrium), Udonella, and Gyrodactylus types of new families, thus increasing the number of families to five. Many additional genera, both old and recently described, were now for the first time placed with the Monogenea. But in the family Polystomidae these authors retained only two genera, Polystoma and Erpocotyle; and in the genus Polystoma was listed only a single species, *P. integerrimum*.

Taschenberg (1879) reverted to the earlier classification of van Beneden and adopted the division of the monogenetic trematodes into two

groups Tristomeae and Polystomeae, which he regarded as families Under the Polystomeae as subfamilies he listed Polystomidae, Octobothridae (= Octocotylidae), Gyrodactylidae, and the new subfamily Microcotylidae; the latter including Microcotyle, Axine, Gastrocotyle and the entirely unlike genera, Aspidogaster, Cotylaspis and Aspidocotyle. To the Polystomidae he added the genera Onchocotyle and Diplobothrium, and in the genus Polystoma included the two species *P. integerrimum* and *P. ocellatum*.

In regard to the previously mentioned forms St. Remy (1891) followed the family and subfamily divisions of Taschenberg, tho adding new genera to each of the subfamilies and removing Aspidogaster, Cotylaspis, and Aspidocotyle from the Microcotylidae. To the Polystomidae, Wright and Macallum had added the genus Sphyranura, and in the genus Polystoma were listed the new species *P. oblongum* Wright and *P. coronatum* Leidy.

Increased knowledge of the trematodes disclosed so many exceptions to their classification according to life history that Monticelli (1892) proposed a new arrangement of the group, based on morphological characters. To contain the forms previously classed as Monogenea, he proposed the suborder Heterocotylea. He raised the Monocotylidae and Gyrodactylidae from subfamily to family rank, making five families in the Heterocotylea. In the family Polystomidae he retained the subfamilies Polystominae, Octocotylinae, and Microcotylinae of former authors.

So far as the Polystomidae are concerned, the synopsis of Pratt (1900) does not differ from that of St. Remy and Monticelli.

Later Monticelli (1903) worked out a new classification of the Heterocotylea, separating the forms on the basis of differences in the adhesive apparatus. He arranged the families in two tribes, Oligocotylea and Polycotylea, the former containing the forms with few suckers and the latter those with many suckers. This division he says is not of great systematic importance but may be of practical value in the identification of families. In the Oligocotylea he included the families Tristomidae, Monocotylidae, Udonellidae, Calceostomidae, Gyrodactylidae, and Dicotylidae; and in the Polycotylea the families Polystomidae, Octocotylidae, Hexacotylidae, Platycotylidae, Pleurocotylidae, and Microcotylidae. Among these the Udonellidae, Octocotylidae, and Microcotylidae are raised from subfamily to family rank, and the Calceostomidae, Dicotylidae, Hexacotylidae, Platycotylidae, and Pleurocotylidae are new families. The family Polystomidae contained the single genus Polystoma with the species *P. integerrimum, P. ocellatum, P. oblongum, P. coronatum,* and *P. hassalli.*

Discussing the classification of Monticelli, Odhner (1912) stated that he considered the number of suckers of secondary importance and the system based on them therefore lacking in fundamental systematic significance. Accordingly he rejected the work of Monticelli, and using the older classification of Monogenea, divided the forms within the group on the basis of differences in the female reproductive ducts. He discussed the relationship of the ducts of the female genital system in various trematode and cestode genera, and stated that he was convinced as was claimed by Stieda that Laurer's canal of the trematodes should be regarded as homologous with the vagina of the cestodes. Intervening authors, Looss (1893), Goto (1894) and several other writers, had considered Laurer's canal of the Malacocotylea as homologous with the genito-intestinal canal of certain Heterocotylea, and not with the vagina of the cestodes. Odhner argued that Laurer's canal was the primitive vagina of the trematodes and that there had been a change of vaginal function from this canal to the terminal part of the uterus, with the resulting degeneration of the former duct. It now served in his opinion only to carry off excess spermatozoa, together with yolk and shell substance not used in the formation of the eggs. He adds that there is no evidence on which to base an explanation of the transfer of the seat of vaginal function from Laurer's canal to the terminal part of the uterus; it must only be accepted as a fact.

According to Odhner, in the group of monogenetic trematodes, two very different structures are included under the term vagina. One present in the Tristomidae, Monocotylidae, and Gyrodactylidae opens to the exterior on the left side of the ventral surface, and at the inner end is enlarged to form the seminal receptacle. This tube he considered homologous to the vagina of the cestodes and Laurer's canal of the digenetic trematodes. The other structures which he did not consider homologous to this true vagina were the ducts of the Octocotylidae, Polystomidae, and Microcotylidae, which function as vaginae and open into the vitelline collecting ducts. These are paired and open to the surface either ventrally, laterally, or dorsally. Contending that they had arisen *sui generis*, he proposed for them the name "ductus vaginalis." Considering the question of whether the paired or unpaired condition of these ducts was primitive, he argued that originally the duct was unpaired and opened ventrally; that the opening became divided and the duct split, therefore the Y-shaped duct of Rajonchocotyle must be considered as a stage in the development of the paired condition of the ducts. A further separation would give the lateral openings of Polystoma. In the Microcotylidae the openings have migrated dorsally and fused producing a single dorsal tube. Odhner could find no homologue for the genito-intestinal canal and since he maintained that it was

not homologous with Laurer's canal, concluded that it had arisen *sui generis*.

On the basis of these differences in the female genital ducts he divided the Monogenea into two suborders: Monopisthocotylea and Polyopisthocotylea. The former is characterized by the absence of the genito-intestinal canal, the presence of a "true vagina" and a single posterior organ of attachment; the latter by the presence of the genito-intestinal canal, "ductus vaginalis," many posterior adhesive organs, and the absence of a "true vagina." In the Monopisthocotylea he included the families Tristomidae, Monocotylidae, Udonellidae and Gyrodactylidae; and in the Polyopisthocotylea the families Polystomidae, Microcotylidae and Octocotylidae. He pointed out that by the removal of the genus Sphyranura, the Oligocotylea, the first of Monticelli's tribes agrees entirely with his suborder Monopisthocotylea. In the second of Monticelli's tribes, however, the Diclidophorinae, together with the genera Dactylocotyle and Hexacotyle, should be removed from the Octocotylidae and placed with the Microcotylidae, since they more nearly agree with the latter forms in internal structure.

The next year Odhner (1913) reaffirmed his idea of the homology of the vagina of the cestodes and Laurer's canal of the distomes, but explained therewith that his denial of the homology of the genito-intestinal canal and Laurer's canal had been based on an error of Cerfontaine in describing an unpaired vagina as present in the genus Dactylocotyle. On examination of this genus he had found that a "true vagina" was absent, and concluded that the "true vagina" of the Monopisthocotylea which he had homologized with Laurer's canal was never present together with the genito-intestinal canal. From this he decided that the "true vagina" was homologous with the genito-intestinal canal and therefore with Laurer's canal. Now maintaining the homology of the "true vagina" and the genito-intestinal canal he is in my opinion obliged to dismiss the presence or absence of the genito-intestinal canal as a basis of difference between his suborders, and explain why in one group this canal opens to the exterior on the ventral side of the body and in the other opens into the intestine. His homology of the "true vagina" and the genito-intestinal canal is a most serious error since it would invalidate the distinguishing feature which separates the two suborders.

I propose to show that the organ which functions as a vagina is homologous in all the monogenetic trematodes, and that there can be no division of the group on the basis of differences suggested by Odhner. In fact, the work of Odhner is based on an incorrect assumption and false homologies. Starting with the assumption that Laurer's canal is homologous to the vagina of the cestodes, he has missed the truth in his

entire discussion and when at a loss to explain a structure has derived it *sui generis*. His later paper (1913) admitting the homology of Laurer's and the genito-intestinal canals corrected one mistaken contention, but his separation of the female copulatory ducts into a true vagina and "canalis vaginalis" seems entirely without foundation. There is no evidence to support the idea that the single vagina is not homologous to the paired vaginae. In fact, Odhner described the paired vaginae as arising by the division of a single unpaired tube, probably ventral in position. He derived this tube *sui generis*, and cited no reason why it is not homologous with the ventral unpaired vagina of the Monopisthocotylea. Further he gives no means of distinguishing between the two.

Looss (1893) presented a strong argument to prove that Laurer's canal is not a vagina, nor homologous to the vagina of the cestodes.

Goto (1894) reveiewed the literature up to that date and gave a careful and detailed study of the *canalis genito-intestinalis*. Making a very clear and comprehensive analysis of the question and summarizing evidence from a wide study of ectoparasitic forms, he concluded that the genito-intestinal canal and Laurer's canal are homologous and that neither are homologous with the vagina of the Monogenea. He showed that in the group there is a perfect series of vaginae from a truly paired to a truly unpaired condition. He discussed the idea of Braun who regarded the presence of a single vagina as the result of a simple atrophy of one of the originally paired vagina, with the conclusion that the relations of the ducts "point strongly to the view that the unpaired vagina has been formed by the union and subsequent displacement of the originally paired vaginae, and not as Braun supposes by the atrophy of one of them."

In the present study, the histological character and the relative position and relationships of the ducts of the female system support the contention of Looss and Goto that Laurer's canal is homologous with the genito-intestinal canal, and affords no evidence that these ducts have any further homologue. A review of the literature and the study of the ducts in the three families discussed in this paper has convinced me that Laurer's canal is homologous to the genito-intestinal canal; and the vagina of the Monopisthocotylea is homologous with the originally single, subsequently paired, and secondarily fused vaginae of the Polyopisthocotylea. It makes no difference whether the single or paired condition is regarded as primitive. Given a single unpaired vagina as described by Odhner for the Monopisthocotylea; by a division of the external part and subsequent lateral migration of the openings, the paired vaginae of the Polyopisthocotylea are explained. These ducts entering the body from the sides, lying parallel with the vitelline ducts and discharging into the

same cavity, became fused at their internal ends with the vitelline ducts and this union continued outward to the location where the vitelline ducts turn toward the follicles and the vaginae branch off to open to the exterior. The advantage of a single duct over two ducts lying side by side is obvious, and the fusion of two parallel ducts is not uncommon in other groups. With a further dorsal migration of the opening of the vaginae there would be a separation of the vitelline and vaginal canals and a dorsal fusion of the vaginae would give the single dorsal vagina of Octobothrium, Axine, and Microcotyle. The earlier fusion of the vitelline and vaginal canals would retard the secondary fusion of the internal ends of the dorsal vaginae and this explains the single dorsal pore and internally paired vagina of *Axine heterocerca* which is used by Odhner as an argument supporting his idea that in the Monogenea two different structures are included under the term vagina.

I agree with Odhner that the seminal receptacles of Sphyranura are homologous to the paired vaginae of Polystoma, and that this furnishes a splendid example of the change whereby the terminal part of the uterus has assumed the copulatory function. It may be that further specialization in this direction, due to the endoparasitic habit and self fertilization, may explain the absence of the vagina of the distomes.

It now remains only to account for the absence of the genito-intestinal canal in the Monopisthocotylea. Odhner stated that this structure is homologous with Laurer's canal, and in his (1912) paper called attention to the fact that Laurer's canal is a "rudimentary organ" which serves no essential function. The vestigeal character of Laurer's canal is believed in by most writers—Looss, Monticelli, Brandes, Goto, etc. This structure is entirely lacking in some distome groups and in others is represented by a blind sac opening from the ootype. Since the genito-intestinal canal is admittedly homologous to Laurer's canal and the latter is known to be a vestigeal structure, it appears reasonable to suppose that it has degenerated in the Monopisthocotylea.

There is a possibility that the Monopisthocotylea instead of having lost a genito-intestinal canal may have arisen from a group of the Turbellaria which had no homologous structure, but this explanation seems very improbable. Haswell (1907) described in certain Australian polyclads a tube which formerly had been considered an accessory or dorsal vagina but which in certain forms opened into the intestine. The presence of this genito-intestinal canal in polyclads, he says, "strengthens the contention, so ably supported by Goto, that the genito-intestinal canal and not the vagina of the Heterocotylea is the equivalent of the Laurer's canal of the Malacocotylea."

The absence of the genito-intestinal canal in the Monopisthocotylea

is undoubtedly a feature of distinct taxonomic importance, and the work of Odhner is an advance step in the formation of a natural system and the final classification of the monogenetic forms. Since the arrangement of Monticelli, based on the character of the adhesive apparatus, so nearly agrees with that of Odhner which in reality is based on the presence or absence of a genito-intestinal canal, it appears that both these features are of large importance in the taxonomy of the group. Present evidence is insufficient to decide which is of greater significance. Further study may show that there is complete agreement in classifications based on both features.

Odhner (1912) argued that the removal by Monticelli of Sphyranura from the family Polystomidae on the basis of the difference in number of suckers was not justified. As previously stated, the writer agrees with Odhner that the seminal receptacles of Sphyranura are homologous with the vaginae of Polystoma, and the agreement in type of genital ducts indicates a closer relationship between these genera than is assigned in the system of Monticelli. Sphyranura undoubtedly should be placed with the Polyopisthocotylea. There are, however, wide and fundamental differences between it and the genus Polystoma, and while future researches may discover intermediate forms which will make it possible to include them with certainty in a single family, for the present such a grouping is hardly justified and the two families should be retained, altho the name Dicotylidae of Monticelli does not conform to the rules of zoological nomenclature.

THE GENUS POLYSTOMA

The family Polystomidae as considered in this paper contains only the genus Polystoma. The members of this genus are widely distributed, species having been described from all the continents except South America. The species are not only widely distributed geographically, but also vary widely in type of host and in location within the host. They are parasitic in the urinary bladder of frogs and toads and on the gills of frog larvae, and also infest the urinary bladder and pharyngeal cavity of many species of turtles.

The structure and development of *Polystoma integerrimum* has been investigated by Stieda (1870), Zeller (1872 and 1876), Willemoes-Suhm (1872), Halkin (1902), Goldschmidt (1902), and André (1910). Zeller (1876) described two forms of *P. integerrimum,* one which became mature in the urinary bladder of the frog, and the other which became mature on the gills of the frog tadpole. These two forms of the parasite show wide differences in size and internal structure. The form which becomes mature in the urinary bladder is much larger, has a lobed testis, external vaginae, and a long coiled uterus which contains many

eggs. The form maturing on the gills of the tadpole has a spherical testis, lacks external vaginae and a long coiled uterus, and has a small uterine cavity in which a single egg develops. Halkin and Goldschmidt have investigated the early stages in this form, but the writer has been unable to find any reference to work on the later larval stages. The findings of Zeller are so unusual that one is led strongly to suspect he confused two different species.

The descriptions of *P. ocellatum* by Rudolphi (1819) and Kuhl and Hassalt (1822) are very brief; that by Willemoes-Suhm (1872) contains one plate, and Looss (1885) figured only the structures at the distal ends of the excretory tubules.

The description of *P. oblongum* Wright (1879) contains sufficiently detailed information for a specific diagnosis and is illustrated by three figures. Stafford (1905) reported *P. oblongum* from the palate of *Chrysemys picta* and the same location in *Chelydra serpentina,* but since Wright originally described the species from the urinary bladder of *Aromochelys odoratus,* Braun reviewing Stafford's article considered the form from the oral cavity as a different species. The form described by Leidy as *P. oblongum,* was reinvestigated by Goto (1899) and proved to be a different species from that described by Wright, but the material he reports was in such a poor state of preservation that renewed study was impossible and so the form must remain unknown.

Leidy's (1888) description of *P. coronatum* is so brief that it is almost valueless; a type specimen mounted as a toto preparation has been available for the present study and many additional points of structure are added to the original description.

P. hassalli was described by Goto (1899) from the urinary bladder of *Cinosternum pennsylvanicum* and has been collected by the writer from the urinary bladder of *Aromochelys odoratus, A. carinatus,* and *Chelydra serpentina,* as well as from *Cinosternum pennsylvanicum.* Additional data correct and supplement the description of Goto.

Johnston (1912) described *P. bulliense* from the urinary bladder of two species of Hyla from New South Wales, Australia. Beauchamp (1913) described *P. alluaudi* from an unknown batrachian from the lower prairies of Kinangop, Africa; the material was collected by the African expedition of Alluaud and Jeannel. Stewart (1914) described *P. kachugae* from the urinary bladder of the water tortoise, *Kachuga lineata,* at Lucknow, India.

In the genus Polystoma present evidence supports the validity of the following described species listed in the order of description:

P. integerrimum Frölich 1791. From the urinary bladder of frogs and toads and the gills of frog larvae; Europe.

P. ocellatum Rudolphi 1819. From the throat and nasal cavity of *Emys europa and Halichelys atra;* Europe.

P. oblongum Wright 1879. From the urinary bladder of *Aromochelys odoratus;* North America.

P. coronatum Leidy 1888. From the fauces of the terrapin; North America.

P. hassalli Goto 1899. From the urinary bladder of *Cinosternum pennsylvanicum, Aromochelys odoratus, A. carinatus, and Chelydra serpentina;* North America.

P. bulliense Johnston 1912. From the urinary bladder of *Hyla phyllochros* and *H. Lesueurii; Australia.*

P. alluaudi, Beauchamp 1913. From an unknown batrachian; Africa.

P. kachugae Stewart 1914. From the urinary bladder of *Kachuga lineata;* India.

In the present work evidence is submitted to justify the inclusion of the following new species:

P. orbiculare Stunkard 1916. From the urinary bladder of *Pseudemys scripta* and *Chrysemys marginata;* North America.

P. opacum Stunkard 1916. From the pharynx of *Trionyx ferox* and *Malacoclemmys lesueurii;* North America.

P. megacotyle Stunkard 1916. From the mouth of *Chrysemys marginata;* North America.

P. microcotyle Stunkard 1916. From the mouth of *Chrysemys marginata;* North America.

With the exception of *P. integerrimum,* the members of the genus are very rarely found and the number of individuals discovered is very small. Wright described *P. oblongum* from two specimens; Leidy, *P. coronatum* from four specimens; Johnston had sixteen specimens of *P. bulliense;* Beauchamp described *P. alluaudi* from a single specimen; Stewart had only two specimens of *P. kachugae.* The writer had only a limited number of individuals of any species; *P. microcotyle* was described from a single specimen; *P. orbiculare* from nine specimens; *P. opacum* and *P. megacotyle* each from three specimens. Because of the limited amount of material, it has been impossible to attempt special technique to differentiate the various organ systems, and the descriptions are therefore incomplete in certain particulars. The general morphological features are however described in sufficient detail that clear specific diagnoses can be made, and in certain instances the finer structure and histology of the organs has been described.

ANATOMY AND HISTOLOGY OF THE POLYSTOMIDAE

The species that have been included in the genus Polystoma show a much wider range of structural variation than is usually present in a natural genus. There are wide differences in the character of digestive and reproductive systems, and variation exists in the type of adhesive apparatus.

There is wide variation in size; *P. integerrimum,* the largest known species measures up to 12 mm. in length, and *P. hassalli* is only 1.3 to 2 mm. in length. The width is one-third to one-fifth of the total length. All the worms that have been included in this genus have a flattened, elongate oval body which at the posterior end bears a large ventral muscular disc or cotylophore. The body is more or less pointed at the anterior end and at the posterior end may or may not have a constriction just before the attachment of the caudal disc. As in all trematodes the shape is subject to considerable variation as the animal elongates and contracts. Locomotion is accomplished by attaching the anterior sucker and then bringing the caudal disc forward; as a result of the terminal attachments and the "looping" method of progression, the dorsal line of the body is more or less arched and the ventral surface is concave. In certain species at the openings of the vaginae on the lateral or ventrolateral margins of the body, there are prominent swellings, the "Seitenwülste" of Zeller. These structures are not present in any of the known North American species.

Organs of Attachment.—The caudal disc bears on its ventral face the chief organs of attachment. These consist of suckers and hooks, the former arranged in pairs, three suckers on each side of the median line. The two posterior suckers are close together and those of the middle pair are separated by a considerable distance, while the anterior pair may or may not be near each other. In all previously reported forms except *P. alluaudi,* the anterior suckers are separated by a considerable distance, giving the disc the shape described by Leidy as cordiform (Fig. 27). In the single specimen of *P. alluaudi* described by Beauchamp, both the caudual and cephalic suckers are separated, while those of each side are contiguous. In *P. orbiculare* the anterior suckers are in the same close proximity as the caudal pair, and each sucker of the disc is separated from the two adjacent to it by uniform distances, making a perfect circle of suckers (Fig. 1). In the six species described by the writer these suckers are complicated structures, set more or less deeply in the parenchyma of the caudal disc. Their structure, character of insertion, muscular attachments, and relation to the surrounding tissue indicate that they are protrusible and retractile, and in fact such movements may be observed by watching the live worm.

The suckers are cup shaped (Fig. 34), and in all the species described in this paper are constructed on an elaborate cuticular framework. According to Zeller the sucker forms as a ridge around a larval hooklet and later sinks into the parenchyma, and this method of origin explains the cuticular covering of the external and internal surfaces of the cup. Running across between these cuticular membranes, there are short refractive fibers which constitute the mass of the wall of the sucker (Fig. 35). Wright and Macallum (1887) describing similar fibers in the walls of the suckers of Sphyranura say, "Instead of the substance of the sucker being formed of muscular fibers disposed in three directions, and capable of modifying the shape of the cavity, as in the distomes, it is not possessed of contractility in Sphyranura (and probably in Polystoma), and is formed of prismatic fibers, rather of a supportive than a muscular character, arranged perpendicularly between the concave and convex limiting membranes of the suckers." Goto (1894) described similar fibers in the suckers of Axine, Microcotyle, Octocotyle, Diclidophora, Hexacotyle, and Onchocotyle and considered them to be more of an elastic than a contractile nature. They are, he states, different from the ordinary muscular fibers of the body and from those of the suckers of the Tristomidae and Monocotylidae, as well as from those of the anterior sucker of Onchocotyle, both in optical characters and in reaction toward staining fluids. The structure of the suckers in these forms and their mode of operation are discussed by Goto at considerable length, but as the suckers he described are constructed on a different type of cuticular framework from that present in the genus Polystoma, obviously the type of suctorial action is different.

In all the species described in this paper, the fibers which form the walls of the posterior suckers are similar to those described by Wright and Macallum and Goto; the cuticular framework is also flexible and elastic, but is of a different type from that described by Goto. In the polystomes investigated by the writer, with the exception of *P. integerrimum,* the sucker consists of three sections or zones which may be designated as basal, intermediate, and external or distal (Fig. 36). The external part or rim of the sucker is supported by numerous cuticular rods formed by the thickening at regular intervals of the cuticular lining. These rods are bent outward, their curvature maintaining the flare of the rim of the sucker. Distally they terminate just inside the rim of the cup and basally they are continuous with and are processes from a band of cuticula which passes around the sucker and separates the external and intermediate portions. In toto preparations this band appears to be divided into sections that are almost square, each with a circular area in the center that increases and decreases in size as the focus is changed.

Sections show that the cuticular lining of the sucker is folded outward against the convex wall with which it is fused, thus interrupting the continuity of the fibrous wall (Fig. 35). The two sides of this invaginated cuticular sac or ring are fused at regular intervals, leaving small pockets alternating with the places of fusion. These small openings in the cuticular band are conspicuous by reason of their different refractive index and show very plainly with a dark field illumination as the square or rectangular sections with the circular areas in the center (Fig. 34). There is apparently no relation between the number of these sections in the cuticular band and the number of cuticular thickenings which serve as supports of the external section.

The middle section of the sucker extends basally from the previously described cuticular band to a somewhat similar evagination of the cuticular lining into the wall of the sucker, but this evagination does not extend to the external cuticular covering of the sucker and only partially divides the fibrous wall. This middle or intermediate portion of the sucker is supported by thickenings of the cuticular lining, processes that extend peripherally from the cuticular band which passes around the sucker at its base. These supporting ridges are not arranged at regular intervals and they are much fewer in number than the cuticular rods which support the external section. They are often branched, tho not more than a single bifurcation was observed.

The basal portion of the sucker is circular, similar in structure to the portions previously described; it has internal and external limiting membranes with fibers extending between. At its center the cuticular and fibrous wall is interrupted and there is the structure described by Johnson (1912) as the connective tissue plug, which appears as a central disc or button, and to which the retractor muscles are attached. This central disc has thickened cuticular edges and bears the larval hooklet. Figure 44 illustrates the method of operation of the suckers. Muscles are attached to the external wall of the distal and intermediate portions of the sucker and the contraction of these muscles retracts the two external zones, with the accompanying protrusion of the basal part. Whether the small hooks at the bases of the suckers are functional is doubtful. As previously described, the cuticular supports do not extend quite to the external margin of the sucker, leaving a soft plastic edge which can be applied all the way around even on an irregular surface. With the contraction of the muscles attached to the basal disc, a vacuum is produced and forms a powerful means of adhesion. Since the walls of the sucker are not contractile and the suckers vary only slightly in size in a single species, the size of the suckers has been used by the writer as a character for determining specific identity.

A cuticular framework similar to that present in Polystoma was described by Wright and Macallum for the suckers of *Sphyranura osleri.* They say: "As the wall of the sucker is itself destitute of contractility, another arrangement exists for modifying the shape of the cavity. Its walls is really divided into three concentric zones, which by special extrinsic muscles can be worked independently. The two circular lines which separate these zones, are marked by an infolding of the investing membrane, which forms a sort of joint, permitting an independent movement of the zones."

The collection of Professor Ward contains a single series of sections of *P. integerrimum* from Germany, and in this specimen the type of skeletal structure just described is absent. Figure 45 shows the character of the suckers in this form. The caudal disc typically bears eighteen hooks. Sixteen are similar in size and shape, arranged as follows: six in a row between the anterior suckers, one situated inside each sucker at the base, and four between the two posterior suckers. In addition to these hooks there is a pair of great hooks, several times the size of the small hooks, between the two posterior suckers. The shape of these hooks and their arrangement are shown in Figures 37 to 43. In many cases there is only one pair of the small hooks between the caudal suckers; in such cases in addition to the great hooks there is a third pair, similar in shape to the great hooks and intermediate in size between the great and small hooks.

The sixteen small hooks are present on the caudal disc of the larva before the suckers are formed and are called larval hooklets by Willemoes-Suhm (1872), but Zeller (1876) says: "Die sechszehn kleinen Häkchen mit ihren Oesen, welche die Haftscheibe angehoren und welche bei der Polystomum larva so ausserordentlich deutlich zu erkennen ist, sind nicht, wie Willemoes-Suhm meint, nur 'Larvalorgane'. Sie werden nicht abgeworfen, sondern sind wie ich auf das bestimmteste wiederholen muss, bei der erwachsenen Thiere noch sämmtlich vorhanden, sehr beweglich und gewiss nicht ohne Bedeutung für ein festeres Anheften." Johnston (1912) in the description of *P. bulliense* says: "Four larval hooklets are present in a row on the ventral surface near the posterior edge of the disc or cotylophore. I have been able to find no trace either in the living worms or the fixed material, of the larval hooklets which *P. integerrimum* and other species bear near the anterior edge of the disc. There is a small anchor shaped hook in the base of each sucker. All these hooks either disappear as the animal increases with age, or very readily become detached. In only one out of sixteen specimens have the whole four posterior hooklets been present; and in only two others were any hooklets at all to be seen. In all other specimens no hooklets could be made out."

In my own material I find that the larval hooklets are invariably present in the bases of the suckers, but of the other larval hooklets, usually several are absent and often those present are so arranged that it is difficult to see how they could function in attachment. Those at the anterior edge of the caudal disc are seldom regularly arranged, and in many cases (Figs. 37 to 43) are in such irregular and unusual positions with reference to each other that the use of one would interfere with the action of the others.

The great hooks are invariably present in the species in which the caudal disc is cordiform in shape, i. e., where the two anterior suckers are separated by a distance exceeding that between the two posterior suckers. In the species *P. alluaudi* and *P. orbiculare* the disc is circular and the great hooks are absent. Usually the cordiform disc is wider and the circular disc is narrower than the body. At first it seemed possible to separate the genus into two subgenera, one in which the disc is circular and the great hooks are absent and another with a cordiform disc and great hooks present, but there seems to be no such clear line of separation. In *P. orbiculare* a large number of chitinous spicules are present on the disc, some between the suckers and the others in the central area of the disc. In *P. opacum* the disc is intermediate in shape; it is difficult to determine whether it is circular or cordiform, and the great hooks are present altho they are not more than half the size of those in other species (Fig. 40). In *P. hassalli* the disc at times may be circular and the great hooks are strongly developed (Fig. 31).

Body Covering.—The body is covered with a non-cellular, unarmed cuticula, which is turned in at the external openings of the various systems. It does not have a uniform appearance but is traversed by lines which extend perpendicular to the surface of the body.

Musculature.—The musculature consists of the dermo-muscular sac, the muscles of the adhesive apparatus, and dorso-ventral strands with much-branched fibers which traverse the body at irregular intervals. The muscles of the body wall consist of an external circular layer, an intermediate layer of diagonal fibers, and inside the latter, bundles of longitudinal fibers. In all the species studied, the inner longitudinal fibers are more strongly developed than either of the other layers. Stieda (1870) in *P. integerrimum* did not distinguish between the two external muscle layers and described only two layers of muscles, an outer layer of annular fibers, some of which were not exactly circular and crossed each other, and an inner layer of longitudinal fibers. Zeller (1876) was in error when he described the diagonal fibers as inside the longitudinal layer in *P. integerrimum.* The arrangement of the muscles of the body wall in Polystoma is the usual condition in the Heterocotylea, and a

similar arrangement has been described in Calicotyle, Axine, Nitzschia, Tristomum, Octobothrium, Temnocephala, Microcotyle, Octocotyle, and Monocotyle. In Diclidophora Goto (1894) described an additional layer of longitudinal fibers between the circular and diagonal layers. He states that in Onchocotyle and Hexacotyle the circular fibers seem to be entirely lacking. In the genus Polystoma there are strong sets of longitudinal fibers near the median line on the ventral side of the body. They could be traced anteriad only to the testis. Posteriad they pass into the caudal disc and together with fibers from the body wall are inserted on the sides and in the bases of the bothria. Muscle strands from both sides of the body pass to each of the suckers (Fig. 29) and smaller groups of fibers from each sucker to each of the others. In addition to the dorso-ventral muscles which extend between various points of the body wall, there are other fibers from the body wall to the internal organs.

Mesenchyma.—The mesenchymal tissue of the body does not show a differentiation into ectoparenchyma and endoparenchyma as described by Brandes (1892) and other writers; it is not of a uniform character, but presents differences in appearance at different points in the same specimen. It may take the form of compact cellular tissue, or of vacuolated cells, or there may be large vacuoles apparently between cells, or the cellular structure may be entirely lacking, there being only a reticulum of fibrous tissue. The parenchyma is traversed by many muscle strands, and the dorsal and lateral regions are occupied by the enormously developed vitellaria (Figs. 19, 23).

Alimentary System.—The digestive apparatus consists of a terminal anterior or oral sucker, a pharynx, a short esophagus and a bifurcate intestine. The oral sucker (Fig. 6) is not fully homologous with that of the distomes. There is no external limiting membrane, branched muscle fibers passing from the inside lining of the sucker to the body wall. Posteriorly it is limited and separated from the body parenchyma by special strands of fibers which pass from the body wall to the wall of the digestive tube and are attached there just anterior to the pharynx. A contraction of these fibers causes the constriction between the anterior sucker and the body parenchyma which is sometimes seen. Longitudinal muscle fibers from the body parenchyma penetrate this posterior boundry of the anterior sucker and pass to the wall of the sucker. Annular muscles, situated just inside the cuticular lining, pass around the sucker from side to side. Situated among the muscle fibers there are large secretory cells. Johnston described the structure as a weakly developed or incipient oral sucker. The anterior sucker, pharynx, and esophagus are lined with cuticula continuous with that of the external surface of the body.

The pharynx is approximately spherical, altho various states of contraction influence its shape to some extent. It does not lie directly in the long axis of the body but obliquely, the lumen extending from the somewhat ventral anterior opening from the oral sucker to a more dorsal posterior opening into the esophagus or intestine. In certain species it is composed of two portions, (Figs. 6, 33) tho both are enclosed in the same external capsule. In the anterior portion there are many strong annular fibers and this part probably acts as a sphincter, altho there are also radial fibers which extend from the external limiting membrane to the cuticula of the lumen. In the posterior part the annular fibers are confined almost entirely to the external region and a small central zone (Fig. 25). The muscle fibers are branched and non-nucleated. Scattered among the fibers in the posterior part there are large nuclei, each with a deeply staining nucleolus and surrounded by a granular or flaky area that is continued by a fine duct traceable by the presence of the same granular substance and leading to the lumen of the pharynx. Goto described somewhat similar nuclei in the pharynx of Diclidophora and regards them as remnants of the cells that have produced the muscle fibers. The writer is inclined to the view that in Polystoma the granular substance is a secretion. No extra-esophageal glands were observed, but that the secretion of the pharyngeal cells is salivary was not demonstrated.

A short esophagus may be present in certain species (Fig. 6) but in most cases the pharynx appears to open directly into the intestine at the juncture of the right and left ceca. There may be a short median or paired lateral pockets of the intestine extending anteriad from the junction of the ceca.

There is wide variation in the type of the intestinal diverticula. In *P. integerrimum* the ceca are much branched and these branches ramify thru the body and the caudal disc (Fig. 45). In *P. alluaudi* the ceca occupy the same location but are merely lobed and have no secondary branches, tho they are united posteriorly. In *P. bulliense,* according to Johnston, "a diverticulum from the buccal cavity runs backwards, ventral to the pharynx, and for a distance equal to its length forming a median unpaired buccal pocket." In all other known species there is a simple bifurcate intestine, the ceca terminating just anterior to the caudal disc. In two specimens of *P. hassalli,* however, the ceca are connected posteriorly; in one of them the ends of the ceca are continuous and in the other there is a connection some distance anterior to the ends of the ceca (Fig. 30). The walls of the diverticula are composed of a delicate fibro-membranous tissue upon which rests the digestive epithelium. The epithelial layer consists of columnar cells whose nuclei lie near the fibro-

membranous sheet and which have large, rounded, often vacuolated bodies extending irregularly into the canal. The protoplasm of the cells is granular.

Excretory System.—In this family as in all Heterocotylea, there are two excretory pores, situated on the dorsal surface about midway between the median line of the body and the lateral edge of the worm, near the level of the caudal margin of the pharynx (Fig. 27, 33). These open from vesicular expansions, which when filled are almost spherical and when empty have folded walls. The descending collecting duct originates in the region of the pharynx from the fusion of smaller ducts and passes posteriad to the region of the caudal disc where it turns cephalad and continues as the ascending collecting duct to open into the excretory vesicle. Both the descending aud ascending ducts receive smaller branches at irregular intervals; at the caudal end of the body a canal joins the tubes of the two sides and a similar connection exists between the descending ducts just anterior to the pharynx. From this anterior communicating canal a branch enters the anterior sucker near the median line. The excretory vesicles are lined with a thin layer of cuticula continuous with that of the external surface of the body and the collecting ducts and accessory branches have a fibro-membranous wall in which nuclei are occasionally embedded. In *P. integerrimum,* Zeller described many connections of the collecting ducts of the two sides thru anastomoes of their smaller branches. He also described cilia on the walls of the collecting ducts. Looss (1885) described the excretory system of *P. ocellatum.* He says the collecting ducts are not ciliated throuout, but only in occasional areas, and describes cilia in the capillaries. These capillaries are long and at the distal end are very much coiled. In this coiled part the capillary is divided so that two flame cells discharge into each coil and are emptied by a single capillary. The caliber of the excretory vessels is very minute, and altho varying somewhat as a result of distention, lacunar expansions were not observed. Because of the limited amount of material, much of which was received in a preserved condition, no attempt was made to trace the excretory system in living worms of this family. The vitellaria completely obscure the excretory ducts in toto preparations. The secondary ducts are so small and so often collapsed that it is impossible to follow their continuity with certainty in sections.

Nervous System.—The morphology of the nervous system of *P. integerrimum* was described in detail by André (1910). He described a supra-esophageal brain from which three pairs of nerves pass anteriad and three pairs posteriad. In another paper (1910a) he gave a detailed description of the eyes of *P. integerrimum.* In the present work no special study of the nervous system was made and no new facts were adduced.

Male Reproductive System.—The testis is a much branched structure in *P. kachugae;* in *P. integerrimum* it is lobed, and in the other known species it is oval or spherical. It is situated near or slightly anterior to the middle of the body. A duct designated an internal vas deferens was described in *P. integerrimum* by Zeller, but Ijima (1884) traced the true relations of this tube and showed that it passes from the ootype to the intestine. Goto (1894) proposed the name *canalis genito-intestinalis* for this structure which is discussed in a later section. The vas deferens arises from the dorso-cephalic margin of the testis and passes dorsad and anteriad. It extends dorsal to the ootype, between the dorsal margins of the ovary and uterus to the level of the genital pore where it turns ventrad and enlarges to form the seminal vesicle (Fig. 13). From the seminal vesicle a duct passes thru the cirrus sac, opening into the genital atrium (Fig. 26). The vas deferens is small and has a fibro-membranous wall, and the seminal vesicle has a lining of columnar epithelium. The cirrus sac is composed of an external muscular wall enclosing a mass of parenchymous tissue which surrounds the ejaculatory duct. This sac is very small in *P. integerrimum* and *P. hassalli.* Ventrally it opens into a common genital atrium (Fig. 26). The ejaculatory duct terminates in the genital papilla, which when retracted is surrounded by a deep depression. In the musculature between this depression and the wall of the cirrus sac are embedded the roots of the genital hooks. When the hooks are retracted there is a shallow depression between them and the wall of the sac. With the contraction of the wall of the cirrus sac the genital papilla and the circle of genital hooks are extruded thru the pore. In most of the species the hooks are sickle shaped with the points projecting outward, and with muscles attached to the outside of the hook at the juncture of the root and shank. These muscles undoubtedly serve as a fulcrum, and the extrusion of the papilla rolls the hooks outward burying their points in the cuticula lining the wall of the vagina of the copulating worm (Fig. 24). In *P. alluaudi* Beauchamp described three genital hooks, *P. integerrimum* has eight, and other species sixteen, thirty-two, and forty. In *P. hassalli* the genital hooks are small, straight and have a wing like process at the middle.

Zeller described a prostate gland in *P. integerrimum,* consisting of masses of large cells situated around the cirrus, and traced ducts from these cells to the lumen of the ejaculatory duct. Johnston in *P. bulliense* says, "Two laterally placed, small groups of gland cells represent the prostate." The statement of Zeller that a gland is present around the cirrus of *P. integerrimum* is certainly correct. In the species described in this paper, a similar gland is present in the parenchyma around the genital sinus. The cells (Fig. 12) are globular or pyriform, stain deeply

and possess a distinct nucleus and nucleolus. Their ducts could not be traced to the ejaculatory duct but in many cases appear to lead to the body wall near the margin of the genital sinus. In *P. orbiculare, P. opacum* and *P. megacotyle* the cirrus sac is large and many nuclei are present around the ejaculatory duct in the dorsal part of the sac. These nuclei are large, with distinct nucleoli, and are surrounded by a deeply staining area of granular or flaky substance, but no cell boundries could be made out.

Female Reproductive System.—In all known species but one, the ovary is oval or comma shaped. In *P. kachugae* it is described by Stewart as a "curved sausage-shaped organ, the curve forming all but a complete circle. The fundus is somewhat bulbous." This structure is usually not more than one half the size of the testis, is situated a short distance anterior to that organ, and in a given species may lie on either side of the body. In all the species studied by the writer it is comma shaped, the larger part is ventral, anterior, and lateral, and terminal region is dorsal, posterior, and mesal. The ova are formed in the large part and the ovary is divided into zones of growth, ova of increasing size being present in each succeeding zone (Fig. 23).

In the species described in this paper the vitellaria consist of masses of follicles occupying the dorsal and lateral regions of the body. Each follicle consists of several cells which may vary much in appearance; the difference is due to the phase of secretory activity of the cells. In the peripheral part of the gland the cells are usually small, with granular or flaky protoplasm, a distinct nucleus and nucleolus; whereas those more centrally located may be two or three times their size, the extra-nuclear area being either vacuolated or filled with droplets of a yellow substance (Figs. 19, 20). In some cells the secretory droplets are scattered uniformly thruout the cell. The presence of the material in the cells often renders the body so opaque that the diverticula can not be seen. The glandular secretion is apparently identical with that which forms the shell of the egg, and this observation further confirms the statement of Goldschmidt (1909) that the so-called vitellaria secrete the shell of the egg. Small ducts from the follicles (Fig. 11) unite and discharge into longitudinal collecting ducts. These extend along the sides of the body, lateral to the ceca and dorsal to the excretory tubules; on either side of the body there is an anterior and a posterior branch which unite just behind the level of the ovary and the common duct discharges into the external end of the vitello-vaginal canal. In *P. bulliense,* Johnston reports: "The lateral vaginal swellings are formed by a large number of papillae, perforated by fine canals, which after a very short course, open into a fairly wide sperm reservoir, situated one on either side, just under the swell-

ings. From these reservoirs, a wide vaginal tube on either side runs backwards and inwards, to open into the anterior lateral yolk duct." A similar condition is described and figured by Zeller for *P. integerrimum*. In all other species in which the structure has been described, the vaginae are open funnels leading mediad and dorsad from their openings on the ventro-lateral surface of the body, and uniting just below the intestine with the common vitelline ducts to form the vitello-vaginal canals. The cuticular lining of the vaginae is very thick and in the parenchyma around the vaginae there are large cells of secretory type (Fig. 24). The vitello-vaginal canals lead medially and unite, either forming a duct which discharges into the ootype (Fig. 32) or opening separately into the ootype (Figs. 3, 16, 24).

From the ovary the oviduct passes posteriad and ventrad, opening into the ootype. Immediately anterior and dorsal to the opening of the oviduct, there branches from the ootype a small tube which after a somewhat twisted double loop opens into the intestine of the side in which the ovary is situated. This genito-intestinal canal has been the source of much controversy and its presence or absence is the diagnostic feature of Odhner's two groups of monogenetic trematodes. Mehlis' gland, the shell gland of earlier authors, is never largely developed and is difficult to find in some specimens where it is represented by a few nuclei in the parenchyma around the ootype. Zeller for *P. integerrimum* and Johnston for *P. bulliense* described prominent "shell glands", and Stewart for *P. kachugae* described "a group of glandular cells found at the same transverse level as the ovary, but on the opposite side of the midline. They appear to be connected with the corresponding vagina, but their function is obscure." Since they are in the precise location of the Mehlis' gland, one is led to suspect that Stewart was confused in regard to the connections and relations of this group of cells, altho in individuals of other species studied by the writer, there are groups of large glandular cells in the parenchyma surrounding each vagina.

The ootype is continued by a tube which passes anteriad on the opposite side from the ovary, and which leads to the uterus. Previous writers have called this tube the oviduct and Johnston (1912) says, "From the ootype, the oviduct runs forward to a point in front of the ovary, whence it bends sharply backwards and runs in a straight course close to the ventral surface, almost to the level of the cotylophore, where it opens into the wide uterus." The use of the term oviduct for the tube leading from the ootype to the uterus is confusing and objectionable. Looss (1899) says, "Der Theil des weiblichen Leitungswegen, der den Keimstock mit dem ootyp verbindet, ist der oviduct oder Keimgang," and this terminology is found in general use thruout the literature. In a large number of trematode genera the ootype opens directly into the

uterus. In the Polystomidae however, there is a definite specialized tube leading from the ootype to the uterus. This duct is not homologous with the oviduct, it is separated from that duct by the ootype, and further, in the specimens examined by the writer the histological character of the two are not precisely the same. The epithelial lining of the oviduct is of the flattened type, and that of the second duct more columnar. Such a duct is present in many cestode genera and is called the uterine duct. The same name is proposed for the tube leading from the ootype to the uterus in the Polystomidae, altho with the understanding that its use is independent of the question of homologies of the female ducts in trematodes and cestodes.

In *P. bulliense* the uterine duct opens into the uterus not at the end but on the side, and there is a posterior uterine pocket. The uterus extends as a wide elongated sac from the extreme posterior end of the body to the common genital sinus. In *P. alluaudi* the intracecal area is occupied by the uterus and eggs are present almost as far posteriad as the caudal union of the ceca. In *P. integerrimum* there is a long uterus which extends in many loops anterior to the ootype, and contains a large number of eggs. In all other known forms, the uterus is situated at the level of the ovary on the opposite side of the body, and contains a single large egg or embryo. Zeller (1876) described a similar condition for the ectoparasitic form of *P. integerrimum*. Figure 14 shows a very early embyro of *P. orbiculare* and Figure 23 a much later stage of development in *P. megacotyle*. No shell is present in the former case, altho it may have been lost in sectioning. There must be some provision for the growth of the embryo and the shell can not be rigid during the uterine period. Where the oviduct arises from the ovary, at its union with the ootype, and at either end of the uterine expansion sphincter muscles produce short contracted portions of the tube. In all the species studied by the writer, with the exception of the vitelline tubules, all ducts of the female system have a fibro-membranous wall and an epithelial lining, which in the ootype, uterine duct, and uterus consists of tall columnar cells with distinct boundries and single nuclei. Describing the epithelial cells lining the ootype in certain other monogenetic forms Goto (1894) says that because of their appearance and reaction to stains he strongly suspects their glandular nature, but since a shell gland is present he can not understand their function. In certain species of Polystoma Mehlis' gland is much reduced or absent, and in these forms the cells of the epithelial lining of the ootype appear to be secretive (Figs. 8, 9). This agrees with the present conception that the vitellaria secrete the shell substance and Mehlis' gland the fluid in which the eggs are suspended.

The genital pore is situated on the ventral surface in the median

line, just posterior to the bifurcation of the digestive tract. It opens from a common genital sinus (Figs. 13, 26) into which the uterus discharges and thru which the cirrus is extruded. The opening from the uterus into the genital sinus is posterior and ventral, while the cirrus sac opens into the dorsal part of the atrium.

When the two specimens of *P. opacum* from *Trionyx ferox* were placed in a watch glass, they soon came in contact and immediately started copulation, the cirrus of each worm was inserted in the right vagina of the other, and the two worms attached to each other, both with the anterior suckers and those of the caudal disc that could be brought in position for adhesion. Attempts to separate the worms failed, so an effort was made to fix them in the copulating condition, but they separated on the application of the killing fluid. This explains the statement of Johnston: "On one side only, in the specimens sectioned, was the vaginal tube filled with sperms; that on the other side was empty." Benham (1901) and Mac Callum (1913) state that copulation in polystomes has been observed only by Zeller.

POLYSTOMA ORBICULARE Stunkard 1916

[Figures 1 to 14]

The material of this species consists of six specimens from the urinary bladder of *Pseudemys scripta* from Raleigh, North Carolina, one specimen from the urinary bladder of *Chrysemys marginata* from Chicago, Illinois, and two specimens from the urinary bladder of *Chrysemys marginata* from Creston, Iowa.

The body is an elongate oval, slightly more pointed anteriorly than posteriorly, and in two of the specimens with slight indentations of the body walls at the vaginae and at the posterior margin of the anterior sucker. These worms (Fig. 1) varied in length from 2.7 to 3.75 mm. and in width from 0.9 to 1.2 mm. The caudal disc is circular, 0.8 to 1.07 mm. in width, and bears the six suckers arranged symmetrically in a circle. The suckers are approximately 0.3 mm. in diameter, and are separated by regular equal intervals. No hooks could be found on the caudal disc with the exception of the single minute larval hooklet in the base of each sucker. These are 0.016 mm. in length and could be seen only under favorable conditions.

The anterior sucker (Fig. 6) is 0.25 to 0.27 mm. in length and 0.37 to 0.42 mm. in width. It opens into the pharynx, a spherical structure 0.24 to 0.28 mm. in diameter. There is a short esophagus visible in sagittal sections altho it is not distinguishable in toto preparations. The ceca meet anteriorly in a wide curve and extend as simple tubes

almost to the posterior end of the body. They have no branches and terminate blindly. In caliber they vary from 0.04 to 0.116 mm.

The testis is spherical or oval, usually slightly longer than broad, and measures 0.29 to 0.39 mm. in width and 0.36 to 0.5 mm. in length. It is near or slightly anterior to the middle of the body. The sperm duct arises at its anterior margin and, lying dorsal to the ootype, passes anteriad. In front of the ovary it turns ventrad and expands into the seminal vesicle. At the outer end of the seminal vesicle the duct is encircled by a sphincter muscle, and then known as the ejaculatory duct passes thru the cirrus sac to open into the genital atrium (Figs. 3, 13). The cirrus sac is almost spherical, and consists of an external muscular capsule filled with parenchymatous tissue enclosing a central canal. In the dorsal part of the sac there are radial muscles passing from the wall to the central duct, and among these fibers a few large nuclei. More ventrally there are sets of muscles developed around the central duct and these are connected to the wall of the sac. Externally the central canal terminates at the apex of a papilla which is separated by a deep depression from the muscular ring that bears the hooks of the genital coronet. This conical muscular ring is protrusible and is separated from the wall of the cirrus sac by a second depression. The invaginations on either side of the genital coronet allow for the extrusion of the coronet of hooks with the genital papilla on the contraction of the wall of the cirrus sac, while the muscles attached to the central canal and the muscular ring bearing the genital hooks serve as retractors. The genital coronet consists of sixteen hooks, similar in size and shape; they have an external sickle-shaped part or shank which turns outward and a root or basal part of about the same length embedded in the musculature (Figs. 2, 13). The basal part is straight and hollow and the internal end is bifurcate. It bears many fine cuticular processes which are particularly prominent near its union with the shank. In the body parenchyma around the terminal part of the cirrus sac there are large unicellular glands (Figs. 12, 13).

The ovary is lateral and may be situated on either side of the body. It is 0.1 to 0.25 mm. anterior to the testis. It is ovoid in shape, with the larger part in which the ova are being formed anterior and ventral, and the oviduct arising from the dorsal posterior region. In sections it appears to be marked into zones, with larger and fewer cells present in each succeeding zone. It is 0.1 to 0.148 mm. in width, 0.14 to 0.185 mm. in length and in one specimen cut in cross sections 0.175 mm. in depth. The oviduct arises as a very small tube and immediately expands (Fig. 3). This expanded portion extends posteriad and ventrad and by means of a short constricted tube opens into the ootype, a specialized region

of the female duct where the vitello-vaginal canals are received and the genito-intestinal canal is given off. The genito-intestinal canal twists in a double loop and then opens into the intestine of the side upon which the ovary is located (Fig. 10). The vaginae are ventro-lateral in position and open to the exterior by funnel shaped mouths. The vitellaria occupy the dorsal and lateral regions of the body; they extend anteriad to the pharynx and posteriad to the caudal disc. There is a strand of follicles across the dorsal side of the body just behind the pharynx, and then the follicles are entirely extracecal in the field anterior to the testis; posterior to the testis the vitellaria overlie the ceca and extend to the center altho they are scanty along the median line. Ventrally the vitellaria are entirely extracecal. Collecting ducts run longitudinally, laterad of the ceca; and just below the cecum of either side the common vitelline ducts formed by the union of the anterior and posterior longitudinal ducts unite with the internal ends of the vaginae to form the vitello-vaginal canals. These canals open directly into the ootype, one on either side, and are thus continuous, forming a canal thru the body from side to side. Mehlis' gland is represented by many nuclei which lie in the parenchyma around the ootype and uterine duct. This latter duct passes anteriad and laterad on the opposite side from the ovary; it is smaller than the ootype in diameter and the epithelial lining is lower. After a slight expansion it is constricted and then opens into the uterus. The uterus contained a single egg or embryo. Figure 14 shows a morula-like mass of cells found in one specimen; in the other specimens there were large spherical eggs, each enclosed in a yellow shell. They vary from 0.21 to 0.24 mm. in diameter.

The excretory system shows no departure from the typical form and while it can not be completely followed in sections, the larger ducts occupy the characteristic positions. The descending collecting ducts arise in the region of the anterior sucker and pass posteriad, lying lateral and ventral to the ceca. They wind back and forth in short curves and at the posterior end of the body turn anteriad and pass in the same winding course to the excretory vesicles. Both descending and ascending ducts receive small branches at irregular intervals. The excretory pores are lateral and dorsal, at the level of the bifurcation of the intestine (Fig. 7).

This species agrees with *P. alluaudi* in shape of caudal disc and absence of great hooks, but differs from that species in type of uterus, number of hooks in the genital coronet, and in the character of the intestinal diverticula and testis. *P. orbiculare* agrees with *P. hassalli* in the number of genital hooks, but the hooks are different in size and shape; *P. hassalli* has the great hooks of the caudal disc well developed

whereas they are absent in this species. In certain particulars *P. orbiculare* resembles *P. opacum,* but the two species have different numbers of hooks in the genital coronets; they differ also in the relative size of caudal suckers. The great hooks of the caudal disc are present in *P. opacum.* The two species differ also in that one is parasitic in the urinary bladder and the other in the oral cavity.

POLYSTOMA OPACUM Stunkard 1916

[Figures 15 to 21]

Two worms of this species were obtained from the esophagus of a single specimen of *Trionyx ferox* from Newton, Texas, and another from the esophagus of *Malacoclemmys lesueurii* from the same region. These trematodes were the same color as the lining of the esophagus and so firmly attached that they were removed only with great difficulty.

The worms (Fig. 15) measured 4, 3.75, and 3.25 mm. in length and 1, 0.85 and 0.8 mm. respectively in width. The body has an elongate oval outline, is flattened dorso-ventrally, and observed in living condition, shows great variations in shape. In an extended condition it narrows at either or both ends, and the contracted form may be not more than half the length when extended, and broadly oval or quadrate in outline. The caudal disc is slightly wider than the body in the mounted specimens, measuring 1.09 and 1.21 mm. in width while each sucker is approximately 0.4 mm. in diameter. The suckers have a chitinous skeletal framework, as is described in the generic discussion. In the external meridinal band there are thirty-two divisions, which number corresponds to the number of hooks in the genital coronet. The suckers are arranged in a circle, altho the anterior pair are separated by a distance slightly exceeding that between the posterior pair. Between the anterior suckers there are many chitinous spicules, and in one specimen two of the larval hooklets. Chitinous spicules are present on the sides of all the suckers and over the ventral surface of the disc. Between the posterior suckers there are three pairs of hooks, viz. two pairs of the small larval hooks and one larger pair, but the great hooks are relatively much smaller than the corresponding hooks in other species in which they are present (Fig. 40). The larval hooklets are 7 to 9μ in length and the great hooks are 75μ in length. The chitinous spicules present on the disc have no definite arrangement and their points may stand in any direction; the three larval hooks between the anterior suckers of one specimen have no definite relative position and their hooks point in different directions; those at the posterior edge of the disc are set

in a row at more or less regular intervals and their hooks all point backward.

The cuticular covering of the body is about 14μ in thickness, and on the contraction of the body is thrown into minute folds and furrows.

The anterior sucker is oval, 0.2 to 0.22 mm. in length and 0.23 mm. in width. It opens into the pharynx (Fig. 18), a spherical structure 0.3 mm. in width. There is a broad nerve commissure crossing the anterior part of the pharynx which contains large ganglion cells. From this dorsal commissure a nerve passes ventrad on either side of the pharynx.

The digestive tract is of the simple triclad type, the pharynx is followed by a short esophagus, 0.17 mm. in length in the sectioned worm, and the diverticula extend as simple tubes almost to the posterior end of the body. They are about 0.15 mm. in diameter and terminate blindly, dorsal to the middle pair of suckers (Fig. 21). The ceca are lateral but close together, separated by only 0.2 to 0.25 mm. They have the usual fibro-membranous coat and epithelial lining, and were empty in the sectioned individual.

The testis is spherical or slightly longer than broad in well extended specimens. It is slightly anterior to the middle of the body and is composed of a large number of lobes or strands of cells, compacted and enclosed in a membranous capsule. Cells with the chromatin of their nuclei in all stages of division and mature spermatozoa were observed in sections. The sperm duct arises at the anterior dorsal margin of the testis and curves dorsad and cephalad. Anterior to the uterus it turns ventrad and expands to form the seminal vesicle. From the seminal vesicle a small ejaculatory duct leads through the cirrus sac and opens into the common genital sinus.

The ovary is ovoid or comma shaped, situated a short distance anterior to the testis, and in all three specimens is located on the left side of the body; but since in other species it may lie on either side, it is probable that the examination of a larger number of individuals would show specimens with the ovary on the right side. In dorsal view it is from 0.16 to 0.2 mm. in length and 0.08 to 0.12 mm. in width, while in the specimen that was sectioned it is 0.08 mm. in width and 0.3 mm. in depth. The oviduct arises at the dorsal posterior margin and curves posteriad, mediad, and ventrad where it opens into the ootype. The vitello-vaginal canals open separately into the ootype, just ventral to the origin of the genito-intestinal canal. The latter duct passes laterad, then dorsad and anteriad, turns mediad almost to the median line of the body, then dorsad and laterad, and opens into the intestine of the side in which the ovary is located. The uterine duct passes to the right

sight of the body, then dorsad and anteriad where it opens into the uterus. Mehlis' gland is present altho not well developed, and the cells are scattered along the uterine duct as well as around the ootype, altho they are not so numerous in the former as in the latter location. The vaginae open to the surface on either side at the ventro-lateral margins of the body, at the level of the posterior margin of the ovary (Fig. 16). On either side the inner ends of the vaginae unite just below the ceca with the common ducts from the vitellaria to form the vitello-vaginal canals. These open separately and directly into the ootype. The vitellaria consist of large compact follicles, underlying the entire dorsal surface of the body from the pharynx to the caudal disc, except the region over the ovary. The vitellaria are reduced and only a few follicles are present in the region over the testis and they are entirely absent in a circular area over the ovary. Ventrally the vitellaria do not extend mediad of the ceca. The vitellaria are so extensively developed that they obscure the internal structures and render the body opaque, and this character suggested the name of the species. Common collecting ducts run longitudinally along the body lateral to the intestinal diverticula and these discharge into the vitello-vaginal canals as previously described. In each of the specimens there is a single large egg in the uterus, and in the one sectioned the uterus extends cephalad of the genital pore and to a point 0.03 mm. from the bifurcation of the intestine. The eggs are broadly oval, 0.25 mm. long by 0.2 mm. wide. The shell is yellow, refractive to light, and apparently composed of the same substance that occurs in small droplets in the vitellaria.

The uterus and cirrus sac open into the genital sinus; the opening of the cirrus is anterior and dorsal to that of the uterus. The common genital pore is situated in the median line, about 0.12 mm. caudad of the bifurcation of the intestine. Embedded in the wall of the cirrus sac and with their points forming the so-called coronet, the genital hooks in appearance suggest the corolla of a flower. There are thirty-three of these hooks in one mounted specimen and thirty-two in the other. In entire length they measure 0.05 mm., the shank or projecting part comprising about half the total length.

P. opacum agrees with *P. alluaudi* and *P. orbiculare* in shape of caudal disc, but *P. alluaudi* has but three spines in the genital coronet, and a long post-ovarian uterus which contains many eggs. *P. orbiculare* has a larger anterior sucker, smaller caudal suckers, a smaller pharynx, fewer vitelline follicles, and only half as many hooks in the genital coronet. *P. opacum* differs from *P. coronatum* and *P. microcotyle* in the shape of the caudal disc and in the reduced condition of the great hooks of the disc.

POLYSTOMA MEGACOTYLE Stunkard 1916

[Figures 22 to 26]

The material of this species consists of three specimens from the mouth of *Chrysemys marginata* from Creston, Iowa. One worm was cut into cross sections and the other two mounted as stained toto preparations.

These worms (Fig. 22) have an elongate ovoid shape. Widest in the region just anterior to the caudal disc, they gradually become narrower anteriorly, and posteriorly they taper rapidly to a caudal tip which is set in the antero-central part of the caudal disc. The worms are 2.5 to 2.7 mm. long and 0.71 to 0.78 mm. in width. The caudal disc is cordiform and the suckers are so large that they slightly overlap each other. The suckers are arranged in about four-fifths of a circle around the lateral and caudal margins of the disc. Measurements thru the disc from side to side at the level of the cephalic suckers are from 1 to 1.4 mm., thru the middle pair 1.2 to 1.8 mm., and thru the caudal suckers 0.68 to 0.7 mm. The disc bears the characteristic armature of hooks. Across the anterior margin there are three larval hooklets in one specimen and four in the other, but their arrangement is not regular or definite and their position would indicate that they do not function in attachment. In the specimen reproduced in Figure 22 the two hooks of the right side have their points almost together and their bases apart. In the bases of the suckers there are small larval hooklets, and one pair similar in size and shape between the two caudal suckers. Also between the posterior suckers (Fig. 41) there is the pair of great hooks and a pair of hooks the same shape as the great hooks and intermediate in size between the great and larval hooks. The hooks measure in length: larval 0.017 mm., great hooks 0.116 mm., and the pair intermediate in size 0.058 mm.

The cuticular covering of the body is approximately 5μ in thickness on the dorsal and 3 to 4μ in thickness on the ventral surface. It is turned in at the external openings and lines the digestive tract to the bifurcation.

The anterior sucker is set off from the remainder of the body by a slight constriction. It is oval, its longest axis crosswise of the body, somewhat flattened posteriorly, and measures 0.28 mm. in length by 0.35 to 0.42 mm. in width. It is followed by the pharynx (Fig. 25) which is 0.35 to 0.38 mm. long, 0.38 to 0.44 mm. broad, and in the sectioned worm 0.34 thick. No esophagus was observed; the ceca meet anteriorly in a wide curve and extend almost to the posterior end of the body. They are 0.06 to 0.11 mm. in diameter, and have an epithelial

lining 0.017 to 0.035 mm. in thickness set upon a fibro-membranous base. The vitellaria are so thick that the diverticula can not be traced in toto preparations.

The testis is situated near the center of the body; it is spherical or oval, 0.28 to 0.33 mm. long, 0.33 to 0.38 mm. wide, and in the sectioned worm 0.28 mm. thick. The course of the vas deferens and the character of the male organs are similar to those in the previously described species. The genital coronet contains thirty-six hooks in one and forty-two in the other toto preparation. They are similar in size and shape, have a straight basal portion with bifid end which is embedded in the wall of the cirrus sac, and a sickle shaped shank which projects into the genital atrium. The basal portion is the same length as the shank and each part measures 0.03 mm.

The ovary (Fig. 23) is a broad comma-shaped organ, situated about midway between the pharynx and testis, on either side of the body. The larger part is anterior and ventral and contains many nuclei of forming ova, and there are zones of developing ova, each with larger and fewer cells until dorsally and posteriorly the oviduct is given off. The oviduct passes mediad, expanding slightly, and then posteriad and ventrad to open into the ootype. This structure is in the ventral part of the body, just anterior to the testis (Fig. 24); from the sides it receives the vitello-vaginal canals and gives off the genito-intestinal canal. This canal after winding in a double loop opens into the intestine on the same side as the ovary. It was empty in the sectioned worm. The external openings of the vaginae are situated on small prominences ventro-lateral in position, altho there is a single large opening to the exterior. The vitellaria consist of masses of follicles occupying the dorsal and lateral areas of the body. They form a sheet of gland cells on the dorsal side of the body posterior to the testis. They are somewhat reduced along the median dorsal area in the anterior half of the worm and entirely absent only in small fields over the testis and uterus. They extend along the sides of the body and ventrally are limited by the ceca. On either side, at the level of the ootype, a common duct from the longitudinal collecting ducts passes ventrad and just below the cecum unites with the vagina of that side to form the vitello-vaginal canal which discharges into the ootype. The uterine duct leads to the uterus, which in each of the specimens contained a large egg. A section of the egg is shown in Figure 23. The eggs are oval, 0.15 by 0.18 mm., and in the sectioned worm the egg is 0.24 mm. in thickness. From the uterus a small duct passes anteriad and ventrad, opening into the genital atrium, posterior and ventral to the cirrus sac.

The excretory system agrees with the general description given.

The descending and ascending ducts are 6 to 11μ in diameter; when empty their walls collapse.

P. megacotyle differs from all known American forms in the large number of hooks present in the genital coronet, and in this character agrees only with *P. ocellatum.* The species differs from *P. ocellatum,* however, in the difference in size of the anterior sucker and pharynx as well as in the size of the caudal suckers. *P. megacotyle* differs from *P. microcotyle* in the number of genital hooks and in the size of the posterior suckers. *P. megacotyle* has a larger pharynx, larger caudal suckers, and a larger number of gental hooks than *P. coronatum.*

POLYSTOMA MICROCOTYLE Stunkard 1916

[Figures 28 and 29]

This species is described from a single specimen from the mouth of *Chrysemys marginata* from Creston, Iowa. The worm was stained and mounted in toto (Fig. 28).

It is 3 mm. long, and 0.78 mm. in width. The caudal disc is cordiform, 1 mm. in width at the level of the anterior suckers, 1.07 mm. thru the middle pair, and 0.74 mm. thru the caudal pair of suckers. Each sucker is 0.28 mm. in diameter and with the exception of the longer distance between the anterior suckers, they are separated by almost regular equal distances. The distance between the anterior suckers is about four times as great as that between the posterior pair. Four larval hooklets are present between the two anterior suckers, three in a row but with their hooks pointing in different directions, and the fourth some distance posterior to the others (Fig. 29). Between the posterior suckers there are three pairs of hooks: the pair of great hooks, one pair of larval hooks, and a third pair intermediate in size between the great and larval hooks. The hooks of this third pair are the same shape as the great hooks. The larval hooks are 0.017 mm. long, the great hooks are 0.116 mm. long, and the pair intermediate in size are 0.061 mm. long.

In this specimen as the suckers are small the musculature of the caudal disc shows very plainly (Fig. 29). Muscle strands from the ventral side of the body and others from the body wall pass to the bases of each of the suckers. Others pass to the outside of the different suckers and are inserted on the distal and intermediate zones of the suckers, serving as retractors in the operation of the organs. Many break up into smaller fibers and can not be traced. From the base of each sucker the muscles spread out in a fan shaped manner and fibers can be traced not only to the large strands from the body wall but also small fibers

pass from the base of each sucker to each of the other suckers. Many of the muscles branch and ramify thru the tissue of the disc.

The anterior sucker is 0.2 mm. long and 0.42 mm. wide; the pharynx is 0.37 mm. long and 0.4 mm. in width. No esophagus is visible in the single toto preparation and only the anterior part of the intestine can be seen.

The testis is slightly anterior to the middle of the body; it is oval, 0.36 mm. in length and 0.42 mm. in width. The sperm duct can be traced dorsally and anteriorly; cephalad of the ovary it expands into a seminal vesicle which stains deeply due to the presence of spermatozoa. The genital coronet contains thirty-two hooks, equal in size and similar in shape.

The ovary is on the left side of the body, about midway between the testis and the genital pore. The oviduct arises at the median posterior margin and passes mediad, but the structure of the ootype could not be made out. The uterus can be distinguished at the level of the ovary on the opposite side of the body and is empty. Laterally the vaginae are visible and the vitello-vaginal canals can be traced mediad a short distance from the ceca. The vitellaria are strongly developed, anteriorly they extend to the middle of the pharynx, and posteriorly to the caudal disc. There is a strand of follicles across the body from side to side between the pharynx and the level of the genital pore. The follicles occupy the dorsal and lateral regions of the body but anteriorly are reduced in the median area and are absent in the fields over the testis and ovary. They obscure the ceca caudal to the testis. No vitelline ducts were seen.

The excretory vesicles appear one on either side of the body dorsally, at the level of the bifurcation of the intestine.

In number of genital hooks this specimen agrees only with *P. coronatum* Leidy. A comparison with a type specimen of *P. coronatum* shows that in the latter form the pharynx and testis are much smaller and the suckers of the caudal disc are much larger.

POLYSTOMA CORONATUM Leidy 1888

[Figure 27]

This description was made from a single type specimen from the United States National Museum. The worm was stained and mounted in toto.

Leidy (1888) says the host is the common food terrapin, and the previous year, speaking of eating terrapin, he mentions *Emys palustris* and *Emys rugosa*. Braun (1879-1893) lists the species from *Cistudo*

carolina. Goto (1899) in discussing the specimen described by Leidy as *P. oblongum*, refers to the food terrapin as *E. rugosa*.

Leidy gives no figure and his description states: "*Polystomum coronatum*. . . . . Body when elongate lanceolate. Caudal disc wider than the body, cordiform, with three pairs of bothria and with the body attached between the anterior two pairs; changeable in form to oblong, circular or quadrate; with three pairs of minute hooks between the anterior part of bothria and with a larger pair and two smaller pairs between the last pair of bothria. Genital aperture with a circular or transverse oval coronet of thirty-two hooks of equal length. No eyes visible. Length, elongated from 4 to 6 mm; contracting to about half the length and widening proportionately."

The specimen from which the present description was made (Fig. 27) is 3.15 mm. long and 0.83 mm. in width. The greatest width is at the level of the vaginae; the body tapers rapidly anteriorly, widening again slightly at the anterior sucker. From the level of the vaginae the body gradually grows narrower posteriorly to its insertion into the caudal disc. The disc is 1.24 mm. wide at the level of the anterior suckers, 1.2 mm. thru the middle pair and 0.78 mm. thru the caudal pair of suckers. Each sucker is approximately 0.37 mm. in diameter, and constructed as previously described. There are thirty-two small divisions in the peripheral cuticular band of the only sucker in which they could be counted. The disc bears the usual eighteen hooks; the six larval hooklets at the anterior margin of the disc are situated in a row equidistant from the anterior edge of the disc, the two lateral hooks on either side are nearer each other than the more centrally located one is to the median one of that side. Larval hooklets are present in the bases of the suckers and one pair is present between the caudal suckers. Between the caudal suckers there are present also both a pair of great hooks and a third pair intermediate in size between the two. The larval hooklets are 0.02 mm. in length, the hooks of intermediate size are 0.051 mm., and the great hooks are 0.132 mm.

The anterior sucker is oval, 0.16 mm. long and 0.4 mm. wide; the pharynx is circular in outline, 0.3 mm. in diameter. No esophagus can be seen in the toto preparation and behind the posterior margin of the testis the ceca are obscured by the vitellaria.

The testis is slightly anterior to the center of the body, circular in outline, and 0.3 mm. in diameter. The vas deferens could not be distinguished; the cirrus sac in ventral aspect is 0.19 mm. in diameter; the genital coronet contains thirty-two hooks, similar in size and shape, the shanks being sickle-shaped.

The ovary is situated on the right side of the body, about its own

diameter anterior to the testis; in ventral view it is circular, 0.094 mm. in diameter. The oviduct passes posteriad and mediad, and the ootype appears as a darkly stained area. The vaginae can be distinctly seen and laterad of the ceca on either side there is a large cavity communicating with the exterior. The uterus is empty; the folded walls of the cavity are visible on the left side of the body. The vitellaria are strongly developed. Masses of follicles occupy the dorsal and lateral regions of the body but ventrally do not extend mediad of the ceca. Anteriorly they extend to the region of the pharynx; there is a strand across the body just behind the pharynx and in the intercecal area anterior to the testis they are largely interrupted, permitting the structures in this region to be made out. None of the vitelline ducts are visible.

The excretory vesicles are anterior to and slightly laterad of the ceca at the level of the caudal margin of the pharynx, but no ducts could be seen.

POLYSTOMA HASSALLI Goto 1899

[Figures 30 to 33]

This species was described by Goto (1899) from the urinary bladder of *Cinosternum pennsylvanicum* from Maryland. The writer has since collected the species from other hosts and localities. A single specimen was found in the urinary bladder of *Aromochelys carinatus* from Newton, Texas; five were collected from the urinary bladder of *Aromochelys odoratus* from Raleigh, North Carolina; two from the urinary bladder of *Cinosternum pennsylvanicum* from Raleigh, N. C.; and three from the urinary bladder of *Chelydra serpentina* from Walker, Iowa.

The worms (Figs. 30, 31) vary from 1.3 to 2 mm. in length and from 0.4 to 0.65 mm. in width. The caudal disc varies in shape from hexagonal to cordiform and is of approximately the same width as the body. The suckers are 0.12 to 0.16 mm. in diameter. The eighteen hooks of the caudal disc have the usual arrangement and are described by Goto. However, he reports the larval hooks as being 0.33 mm. in length and the great hooks between the caudal suckers as 0.125 mm. in length. This is evidently a typographical error, since he figured the great hooks as about four times the size of the small ones. In the present material the great hooks are the same length as stated by Goto and the smaller ones are 0.033 mm. in length, which agrees with the figures of Goto by a change of one place in the decimal point.

The anterior sucker is ovoid, more pointed anteriorly. It may be longer in either the anterior-posterior or lateral axis and varies in diameter from 0.22 to 0.33 mm. The pharynx is spherical or oval and varies

in width from 0.1 to 0.14 mm.; it may be longer in either axis. There is no esophagus, but in some specimens a median pocket of the intestine extends anteriad from the bifurcation to the pharynx. In others, and this is a more usual condition, lateral pockets of the intestine extend anteriad, one on either side of the pharynx (Fig. 33). The anterior sucker and pharynx are lined with cuticula; the intestine with the usual digestive epithelium. In those specimens in which the uterus contains an egg, the large size of the egg causes the ceca to be widely separated at the uterine level and they approach each other behind the uterus. In one specimen, median branches from the two ceca fuse and form a posterior connection of the diverticula (Fig. 30), and in another the two ceca are united at their ends.

The testis is situated ventrally, just behind the middle of the body. It is a somewhat shapeless mass, roughly oval in outline, crosswise of the body, extending between the ceca just posterior to the uterus. The vas deferens passes anteriad, dorsal to the ovary and between it and the uterus; anterior to the uterus the sperm duct turns ventrad, enlarges to form a seminal receptacle, and then passes thru the cirrus sac, opening into the genital atrium (Fig. 32). The cirrus hooks are sixteen in number, 0.028 mm. in length, straight, and with a wing like process at the middle as described by Goto.

The ovary is comma shaped or ovoid in outline, situated obliquely in the body, on either the right or left side. Typically the ovary is on one side of the body and the uterus on the other, but the enormous size of the egg causes the uterus to occupy a more or less central position, crowding the ovary far to one side. The ovary is 0.058 by 0.065 mm. in the smallest and 0.085 by 0.12 mm. in the largest worms, altho the size of the ovary does not correspond precisely with the size of the worm. The oviduct arises at the dorsal median and posterior part of the ovary and after a dorsal loop it turns posteriad and ventrad to open into the ootype. Mehlis' gland is present. The genito-intestinal canal branches from the ootype and after a short winding course opens into the intestine near the ovary. From the ootype, the uterine duct passes laterally to the opposite side of the median line and then anteriorly and dorsally to open into the dorsal posterior part of the uterus. The vitellaria extend from the pharyngeal region to the anterior margin of the caudal disc; there is a row of follicles across the dorsal surface behind the pharynx but they are absent between the ceca anterior to the testis. According to Goto, "lobes not very numerous, separated from one another, mostly confined to the lateral portion of the body, but also present in the median portion behind the testis." The vaginae are ventro-lateral, midway between the anterior and posterior ends of the body. There are no vaginal prominences, the vaginal openings are

single, and internally they unite with ducts from the longitudinal vitelline ducts to form the vitello-vaginal canals, as described for the other species. They do not open separately into the ootype, but the two vitello-vaginal canals open into a common reservoir from which a duct passes dorsad and discharges into the ootype (Fig. 32). In a few of the specimens the uterus is empty and in others it contains a single large egg, the size of which varies within wide limits. The smallest eggs are 0.11 by 0.25 mm. and the largest 0.18 by 0.34 mm. The posterior edge of the uterus is at the level of the vaginae, and anteriorly there is a small duct from the uterus to the ventral posterior part of the genital atrium. The genital pore is in the median line, a short distance posterior to the bifurcation of the alimentary tract.

The excretory pores are slightly more posteriorly situated than in the previous described species. Descending and ascending ducts occupy the characteristic positions.

POLYSTOMA OBLONGUM Wright 1879

This species was described by Wright (1879) from the urinary bladder of *Aromochelys odoratus*. I have had no opportunity to work on material of the species and the following discussion is based on the description of Wright. According to that author *P. oblongum* measures up to 2.5 mm. in length and 1.5 mm. in width. The body is oblong in shape, tho capable of considerable variation. The caudal lamina is somewhat narrower than the greatest width of the body and is shorter than broad. The arrangement of the suckers and hooks is similar to that in *P. integerrimum;* the suckers are 0.2 mm. in diameter; the large hooks are 0.15 mm. and the small hooks are 0.015 mm. in length.

The mouth is on the ventral surface of the rounded anterior end. The pharynx is bowl-shaped and the intestinal ceca are without anastomoses or branches. The description of the excretory system is very meager; concerning it he says that only the convoluted lateral stems were observed near the anterior end.

The testis is situated in the posterior third of the body, the vas deferens passing dorsad and anteriad to the genital pore, which lies immediately behind the bifurcation of the intestine. The cirrus coronet is described as consisting of sixteen alternately large and small hooks. The free end of each is sharply curved, while the attached end is shaped like a cross the transverse piece of which is longer on one side than the other. The longer pieces measure 20μ and the shorter ones 15μ.

Doubt is expressed concerning the disposition and relations of the female organs. The ovary is described as situated in front of the testis on the right side of the body, but it seems probable that the organ figured

as the "(shell gland?)" is really the ovary. The lobes of the vitellaria are scattered and extend from the pharynx to the caudal lamina or disc. It is doubtful whether Wright was correct in his statement that "The transverse duct seemed to pass inward dorsally from the intestinal ceca," since in all other known species the vitelline ducts are ventral in position.

The uterus is described as containing a single large egg or embryo. The egg shell is thin and is destitute of the short stump present in that of *P. integerrimum,* but has a rather large operculum. In two cases the embryo had already escaped from the shell and moved actively within the uterine chamber. It is a Gyrodactylus-like larva, similar to that of *P. integerrimum,* with eye spots disposed in the same fashion. It is devoid of cilia, and movement seemed to depend entirely on the muscles and hooks of the caudal disc. The latter had a rounded outline except posteriorly where there was a square projection bearing the four small posterior hooks. The disc measured 0.114 mm. across and the twelve small anterior hooks were disposed at regular intervals on the margin of the rounded part. There was no trace of suckers. The small hooks had already attained their definitive size and form. The two large hooks were situated considerably further in from the margin than in the adult, and measured only 0.024 mm. instead of 0.15 mm. in length, which difference it is stated was due to the shortness of the immersed portion, in which, however, the notch was already formed.

In shape, as well as relative position and size of organs, *P. oblongum* strongly resembles *P. hassalli.* It is significant also that both are from the urinary bladder of *Aromochelys odoratus. P. oblongum* is slightly longer and broader than *P. hassalli,* the posterior suckers are larger and the small hooks of the disc are only about half the length of those in those in *P. hassalli.* The two species agree in number of genital hooks, but in the former species the hooks are alternately large and small and with the free end sharply curved, while in *P. hassalli* they are straight and uniform in size.

The species in the genus Polystoma have been arranged in the form of an analytical key utilizing the more prominent or more useful diagnostic structures in separating the different forms. This key is found on the following page.

KEY TO THE SPECIES OF THE GENUS POLYSTOMA

1	(6)	Uterus long, contains many eggs 2
2	(5)	Great hooks present on the caudal disc 3
3	(4)	Ceca branching ..... *P. integerrimum*
4	(3)	Ceca not branching ..... *P. bulliense*
5	(2)	Great hooks not present on caudal disc ..... *P. alluaudi*
6	(1)	Uterus short, contains a single egg 7
7	(22)	Great hooks present on caudal disc 8
8	(21)	Genital hooks of equal length 9
9	(12)	Not more than sixteen genital hooks 10
10	(11)	Genital hooks eight in number; ectoparasitic form ..... *P. integerrimum*
11	(10)	Genital hooks sixteen in number ..... *P. hassalli*
12	(9)	Genital hooks more than sixteen in number 13
13	(16)	Genital hooks thirty-two in number 14
14	(15)	Caudal suckers large, adjacent but not contiguous, pharynx, smaller than anterior sucker ..... *P. coronatum*
15	(14)	Caudal suckers small, widely separated, pharynx equal in size to anterior sucker ..... *P. microcotyle*
16	(13)	Genital hooks more than thirty-two in number 17
17	(20)	Testis simple 18
18	(19)	Caudal suckers large, overlap ..... *P. megacotyle*
19	(18)	Caudal suckers small, separated ..... *P. ocellatum*
20	(17)	Testis branched ..... *P. kachugae*
21	(8)	Genital hooks unequal in length ..... *P. oblongum*
22	(7)	Great hooks of caudal disc reduced or absent 23
23	(24)	Genital hooks sixteen in number ..... *P. orbiculare*
24	(23)	Genital hooks thirty-two in number ..... *P. opacum*

ASPIDOGASTRIDAE

Because of its peculiar multiloculate adhesive apparatus, Burmeister (1856) called attention to the difference between the genus Aspidogaster and the remainder of the trematodes, and suggested a division of the Trematoda into (1) Malacobothrii for the distomes and holostomes, (2) Pectobothrii for the polystomes, and (3) Aspidobothrii for Aspidogaster. Subsequent writers however continued to include Aspidogaster with the polystomes until Monticelli (1892) revived the classification of Burmeister, but named the three suborders into which he divided the trematodes, Heterocotylea, Aspidocotylea, and Malacocotylea.

In the classification of Monticelli, the Aspidocotylea contained the single family Aspidobothridae. Poche (1907) proposed to make the name of the family agree with the rules of zoological nomenclature according to which "The name of the family is formed by adding the ending -idae to the stem of the name of its type genus." Thus the name of the family must become Aspidogastridae.

The family is of special interest to students of trematode morphology. The form of the adhesive apparatus, with its retractile marginal organs, the separation of the body into dorsal and ventral portions by a muscular partition, the sac-like alimentary tract, and the details of the genital organs are peculiar to the group. The family contains both ectoparasitic and endoparasitic species, forms with direct development and at least one species which has an intermediate host, while the hosts infested by the adult parasites include both invertebrates and vertebrates, species having been reported from molluscs, fishes, and turtles.

Summaries or revisions of the group have been made by Diesing (1850, 1859), Taschenberg (1879), Hoyle (1888), Monticelli (1892), Braun (1879-1893), and Nickerson (1902).

Only three species representing two genera of the family are known from North America, *Aspidogaster conchicola* von Baer 1827, *Cotylaspis insignis* Leidy 1856, and *Cotylaspis cokeri* Barker and Parsons 1914. Representatives of each of these species were available for the present study. The first two species are well known; concerning *A. conchicola* no further data were obtained, but a few corrections are made to former descriptions of *C. insignis*.

Cotylaspis cokeri has been mentioned but once in print, but on the basis of extended studies this form had been fully described and its position as a new species demonstrated in a thesis submitted by the writer in partial fulfillment for the degree of Master of Arts in the Graduate school of the University of Illinois in June 1914. The following October Barker and Parsons (1914), having also been working on this form independently, published a brief description naming it *Cotylaspis cokeri*. Since I had completed my work on it before the appearance of their note and the publication of their final report has been delayed it seems proper to give here a detailed description of the species.

ASPIDOGASTER CONCHICOLA von Baer 1827

About fifty specimens from the pericardial and renal cavities of *Andonta corpulenta* from Havana, Illinois, and a similar number of specimens from the same organs of *Quadrula undulata* from North Judson, Indiana, constitute the material of this species available for study.

A detailed comparison of these specimens with the descriptions of *A. conchicola* as given by Voeltzkow (1888), Stafford (1896), and other writers, shows that they belong to that species and substantiates the observations of Leidy (1851), Kelly (1899), and Kofoid (1899), that *A. conchicola* occurs in this country. So far it is the only species in the genus known from molluscan hosts.

Kelly (1899) made a parasitological examination of 1537 individuals of forty-four species of unios from Mt. Vernon, Iowa, Havana, Illinois, and Lewisburg and Phoenixville, Pennsylvania, and included in his report results of the examination of seventy-seven individuals belonging to eighteen species, made by Kofoid in 1895 and 1896. In four hundred thirty-five cases *A. conchicola* was found in the pericardium only, in seventy-five in the kidneys only, and in one hundred thirty-four cases both cavities contained the parasite. The presence of the mature trematode in the pericardium and of eggs within the nephridia was not infrequent. Of the 1537 specimens examined, forty-one per cent were parasitized with *A. conchicola* and thirty-seven of the forty-four species were infested with the parasite.

No further data on this species were obtained by the present study.

COTYLASPIS INSIGNIS Leidy 1856

[Figure 56]

The material of this species consists of specimens from *Anodonta imbecilis, A. corpulenta, Lampsilis gracilis,* and *Unio pustulosis* from Havana, Illinois, and others from *Anodonta ferrus* and *A. ovata* from Reed's Lake near Grand Rapids, Michigan. The material proved to belong to the same species and was identical with *C. insignis* Leidy.

Leidy first discovered the parasite in the Unionidae of the Schuylkill River and founded the genus to receive the new species. His generic and specific diagnosis (1858) follows: "Body curved infundibuliform, anteriorly cylindro-conical, posteriorly expanding into a subcircular or oval ventral disc with numerous acetabula arranged in a triple series. Mouth infero-terminal, with prominent upper lip, and protractile into a cup or disc like acetabulum. Intestinal apparatus as in Aspidogaster, eyes two, distinct, black, situated on either side of the head. Generative apertures inferior between the head and ventral disc."

According to the same author, *C. insignis,* the type species is: "Translucent white or pink white, upper lip snout like, conical, ventral disc crenate at the margin: acetabula twenty-nine, oblong quadrate, the outer rows continuous in front and behind forming a circle. Length from one-half to one line; ventral disc from one-fourth to one-half line in diameter. Adheres to the outer surface of the renal organ and upper margin of the foot, within the cleft of the upper branchial cavity of *Anodonta fluviatilis* and *A. lacustris.*"

Forbes (1896) reported this parasite in the river clams at Havana, Illinois. Osborn (1898) described the species from Lake Chautauqua, New York, as *Platyaspis anadontae.* Kofoid (1899) corrected this error, demonstrating that Leidy's genus is entitled to recognition, and establishing the specific identity of *Platyaspis anadontae* Osborn with *C. insignis* Leidy. Kelly (1899) reporting on the examination of over sixteen hundred individuals of forty-four species of Unionidae found the parasite in twenty-four different species of molluscs and in eighteen per cent of the individuals examined.

Osborn (1904) gives a review of the literature, an account of the distribution, habits, external and internal anatomy of the mature worm, and a description of a very young individual. The young specimen described has a simple ventral sucker, no eye spots, no marginal organs, two entirely distinct excretory systems, and wholly separate pores. This condition of the excretory system is compared with the condition in redia and cercaria and according to Osborn favors the idea suggested by Leuckart that the Aspidogastridae are sexually mature redia.

COTYLASPIS COKERI Barker and Parsons 1914

[Figures 46 to 55, 57, 58]

From four to twenty-five specimens were found in the intestine of each of seven specimens of *Malacoclemmys lesueurii* from Newton, Texas.

The worms (Figs. 46, 47, 52) average 1.5 mm. in length by 0.7 mm. in width, altho there is considerable variation in relative length and width due to the movements of the animal. The body is composed of two parts, an anterior dorsal forebody and a posterior ventral adhesive disc. When extended (Fig. 46), the forebody has the shape of a cornucopia, the larger end attached obliquely to the central two-thirds of the dorsal surface of the adhesive disc. In this condition the worm has an elongate form, projecting beyond the adhesive disc a distance equal to the length of that structure: in a retracted condition (Fig. 52) it is compact and may not project beyond the disc. The total length of the worm varies therefore with the state of extension of the forebody, from the length of the adhesive disc to twice that distance.

The adhesive disc (Figs. 47, 57) is a muscular organ, a multiloculate sucker, used for attachment and locomotion. It has a crenate oval outline, the dorsal surface is arched, and the ventral surface is flattened. The ventral surface is divided by two longitudinal and eleven cross ridges into thirty-two acetabula, which are arranged in three rows; there are twenty-two peripheral alveoli enclosing ten median alveoli. In this statement, the alveolus at either end is counted in the peripheral rather than the median row, tho in location included in both. These compartments change in shape with the movements of the animal, becoming oval or quadrangular. The shape and size of the disc are relatively constant, measurements of the disc in twenty mounted toto specimens vary only from 1.2 to 1.4 mm. in length and from 0.58 to 0.78 mm. in width. This structure recalls the molluscan foot, and it has often been termed the foot altho the morphological comparison is not precise.

Movement consists of extension of the forebody, which furthermore may be turned in any direction, and in the less striking and more restricted movement of the disc. The disc has a tendency to turn up at the edges, especially at the anterior and posterior ends. In adhesion the organ may act as a unit, or the separate alveoli may function independently. In locomotion there is a regular series of movements, the forebody is extended and attached by the sucking action of the mouth funnel, then the disc is loosened and the forebody contracted, bringing the anterior part of the disc near the mouth, when the disc is attached

and the series of movements repeated. The worm moved rapidly across the field of the microscope.

Body Covering.—Externally the worms are covered by a non-cellular cuticula, which is thickest on the dorsal side of the body and thinnest on the ventral surface of the adhesive disc (Figs. 49, 53). It is without hooks or spines, and on the dorsal surface reaches a thickness of 5μ, while on the ventral surface of the disc it is only about 1μ in thickness. The cuticula is turned in at the external openings and lines the external portions of the canals of the alimentary, excretory and reproductive systems.

Musculature.—Immediately inside the cuticula is the three layered dermo-muscular wall, circular longitudinal and oblique muscles occurring in the order mentioned, the circular lying next to the cuticula and in all parts of the wall being better developed than the others. The musculature is delicate and in some places the longitudinal and oblique muscles are very scanty. The musculature of the ventral side of the forebody is continued posteriorly in a thin sheet, the so-called septum or diaphragm (Fig. 53), which lies just above the limiting membrane of the musculature of the disc and extends posteriad as far as the caudal end of the cirrus sac. In *C. insignis* Osborn described this structure as passing posteriad as far as the caudal end of the ovary and in other genera it is more strongly developed. The parenchymous muscles of the body are long, often much branched, and most abundant in locations where they connect different parts of the body wall with each other or with adjacent internal structures. In the anterior part are many well developed muscles of this type used in the movement of that region. Running longitudinally among the vitellaria, as well as dorso-ventrally among the viscera there are many muscle fibers. Sphincters and dilators occur at the genital pore, excretory pore, at the base of the mouth funnel, and at the opening between the pharynx and the intestine.

The disc is separated from the forebody by a limiting membrane (Figs. 49, 53). This membrane runs parallel to the general course of the external ventral surface of the disc, projecting ventrad at each ridge. Extending between this membrane and the external wall there are muscle fibers, often much branched especially at the ends. The ventral projections of the limiting membrane into the ridges of the disc form two sides of long triangular prisms, which extend longitudinally and transversely above the musculature of the disc. One face of each of these prisms is dorsal and the opposite angles extend ventrad forming the ridges which separate the disc into fossettes. These ridges are composed of fibrous connective tissue in which a few nuclei are embedded.

Alimentary Tract.—The mouth funnel is a cup shaped muscular structure (Fig. 51) which functions as an organ of adhesion. There is no oral sucker. The mouth funnel is 0.08 to 0.1 mm. in diameter, sub-terminal in position. There is no prepharynx, the mouth funnel opens directly into the pharynx. The latter is a spherical muscular organ 0.09 to 0.1 mm. in diameter. As described by Osborn for *C. insignis,* it is followed by a very short esophagus, which in the anterior part has a cuticular lining and in the posterior part where the esophagus passes over into the intestine, a lining of flattened epithelial cells. The intestine is an elongate sac or tube extending on the dorsal side of the body 0.1 to 0.2 mm. posterior to the caudal edge of the testis. It varies but slightly in caliber, averaging about 0.075 mm. in diameter. The wall consists of a fibro-membranous sheet upon which rests a layer of columnar epithelial cells. The large deeply staining nuclei of the epithelial cells lie in the basal part while many delicate elongate processes extend out into the lumen of the canal.

Male Reproductive Organs.—The testis is large, single, median, its anterior margin lying at the center of the adhesive disc. It is almost spherical and measures 0.25 to 0.35 mm. in diameter. Cells of various sizes and with the chromatin material in various stages of division, as well as mature spermatozoa are to be seen in sections. The sperm duct arises at the anterior part of the testis and turns to the left, entering the side of a long, much-coiled seminal vesicle (Fig. 48). This vesicle is a large tube, 0.1 to 0.175 mm. in diameter, extending from the region of the testis to the cirrus sac. It is coiled eight to sixteen times and in all mature specimens is filled with spermatozoa. Terminally it is constricted into a small tube which enters the large cirrus sac. This latter structure (Fig. 53) is 0.145 to 0.2 mm. wide and 0.2 to 0.25 mm. long, has a strong muscular wall, and is pyriform in shape, the smaller end opening anteriorly at the genital pore. Inside the cirrus sac there is a dilated, curved portion of the duct which has muscular walls and is lined with epithelial cells. Surrounding the duct and filling the cirrus sac are the large cells of the prostate gland. These are pyriform and average 26μ long by 17μ wide. In living specimens the cirrus was observed in the extruded condition.

Female Reproductive Organs.—The ovary is a small organ, ovoid in shape, averaging 0.16 mm. in length, 0.1 mm. in width, and 0.05 mm. in thickness. It is located (Figs. 46, 52) at the right of the median line, slightly anterior to the middle of the body. The oviduct arises (Fig. 48) at the posterior ventral margin of the ovary and passes posteriad; receives a short common vitelline duct, and then expands into two or three irregular enlargements. Mehlis' gland is present, the

nuclei lying in the parenchyma around the ootype. The uterus passes posteriad on the lateral side of the collecting duct of the excretory system as far as the caudal end of the testis where it turns to the median line. It passes ventrad and anteriad beneath the testis; in front of the testis it turns dorsad and toward the ovary, but just before reaching the ovary it turns and crosses to the opposite side of the body and then passes with little deviation to the genital pore. There is a strong sphincter at the distal end of the uterus (Fig. 54). Eggs were present at various places in the course of the uterus and when the worms were placed in tap water, the eggs near the pore were extruded. The eggs are few in number, not more than six being present in any specimen. They vary from 0.071 to 0.086 mm. in width and from 0.137 to 0.145 mm. in length. The average of twenty-five is 0.075 by 0.141 mm.

The vitellaria (Figs. 46, 49) are arranged along the sides of the body, extending from the posterior end to the level of the cirrus sac. The follicles are more numerous and closer together in the posterior region, gradually becoming fewer in the anterior part of the vitelline zone. They lie just above the limiting membrane which forms the dorsal boundary of the musculature of the adhesive disc, and number up to forty on each side. They vary in size, measuring from 10 to 40μ in diameter. In some specimens they appear to be arranged in a double row on each side with the follicles placed alternately, but there is common and wide variation from this condition. Collecting ducts extend along the median face of the vitellaria and at the level of the ootype pass mediad where they unite to form a small receptacle which empties into the ootype. In *C. cokeri* the vitelline follicles are smaller and fewer in number than in *C. insignis.*

The genital pore (Fig. 54) is double, situated in the median line on the ventral side of the forebody, dorsal and anterior to the adhesive disc. There is no genital atrium, the two ducts open to the exterior separately, the opening of the cirrus sac is on the right and that of the metraterm is on the left. Barker and Parsons described a genital atrium opening thru a common pore, but I fail to find such a structure. In *C. insignis,* Osborn described a single genital opening and a genital atrium, but in sections of *C. insignis* I find the same condition as in *C. cokeri.*

Excretory System.—Most of the observations on this system were made on living specimens. As the water evaporated from under the coverglass the worm was flattened and the larger excretory tubules could be easily followed. The pore (Fig. 50) is median, dorsal, near the posterior end of the body. There may or may not be a small papilla-like prominence around the pore. There is a single excretory vesicle,

situated between the large flask like ends of the collecting ducts and the pore. In the pulsations of this organ, the anterior ventral part contracted and the constriction passed posteriad and dorsad, expelling the fluid thru the pore. The two collecting ducts extend cephalad from the excretory vesicle, one on either side of the forebody, median to the vitellaria. Just posterior to the pharynx each duct divides, sending a branch cephalad on the lateral side of the pharynx and anterior sucker, and a second branch turns caudad. This caudal branch subdivides into a branch leading to the region of the genital pore, and a longer larger branch which passes posteriorly to the region of the testis and receives many smaller side branches. Cross sections (Fig. 49) show the collecting ducts to be dorsal in position. In morphological and histological features the excretory system of *C. cokeri* is similar to that of *C. insignis*. Osborn gives a comparison of the excretory system in that species with the same system in other genera of the family.

Sensory Structures.—There is a dorsal nerve commissure crossing the anterior part of the pharynx, and nerves were traced running cephalad and caudad from it. In about half of the specimens mounted in toto, a pair of black pigment spots is present on the dorsal commissure. In others only a single spot is visible and in a few specimens none could be found. In all the sectioned worms, however, both "eye spots" were observed, altho in some they were very small and difficult to find. These structures are dorsal and anterior to the pharynx (Fig. 58) and consist of a large number of black pigment granules. No lens is present. Barker and Parsons report that eye spots were not found.

At the ends of the cross partitions of the adhesive disc are the marginal organs (Fig. 55). These structures occur in the interstices between the muscular ridges of the ventral disc and its peripheral wall. Such an organ consists of a fine tube about 20μ in length and 1μ in diameter, leading dorsad from the ventral surface of the ridge and terminating in a large spherical cavity in the form of a bulb. The entire organ is lined with cuticula, continuous with that of the external surface of the body. The external half of the canal possesses a thick wall composed of annular muscles, while the internal portion has a thin wall with a few annular fibers and is often curved or looped. At the external end of the inner portion there is a flask-like enlargement which is connected with the heavy walled region by a short constricted portion about 2μ in length. Longitudinal fibers pass from the wall of the distal part of the canal to points near its inner end or to the wall of the cavity. This latter structure is spherical or oval 15 to 20μ in diameter, and empty in most of the sections. It has a fibro-membranous wall and in a few cases is filled with homogenous granular substance or fluid. In other sections

the bulb contains a few granules or "concretionary bodies", but in structure these appear identical with the cuticular lining of the cavity. As mentioned above the organs are located in the angles between the muscular ridges and the wall of the disc, and are set in a mass of non-staining fibrous connective tissue. Some of the fibers pass dorsad from the bulb between the muscular ridges to the limiting membrane of the disc, but in appearance these are similar to the others and there is nothing to indicate that they are nervous in character. However in one section, stained with Heidenhain's iron haematoxylin, there is a nerve fibril passing around the bulb and terminating on the inner end of the heavy walled portion of the canal (Fig. 55). Other nervous structures were not observed. The connective tissue contains many nuclei, similar in size and shape, and in no case was a connection between these nuclei and the marginal organ observed. No glandular cells and no evidence of a secretion were found. In the study of living specimens it was noted that the marginal organs were everted and retracted as the worm moved. Everted they appeared as membranous sacs and their movement was rapid and precise. No evidence was found to indicate that these organs possess a glandular function; the character of their movement and the nerve fibril leading to the canal as demonstrated incline the writer to regard these structures as sensory.

Similar organs have been reported as present in all the genera of the family except Stichocotyle. They were first noted in Aspidogaster by Dujardin (1845) who described them as pores or orbicular glands. Voeltzkow (1888) observed in Aspidogaster that they were protrusible and retractile, and for this reason decided they were sensory. Monticelli (1892) described them in *Cotylogaster michaelis* and supported the idea of their sensory character. Nickerson (1902) described in *Cotylogaster occidentalis* a bundle of fibers which he regarded as a nerve entering the bulb at its basal end, and a cluster of bipolar nerve cells lying upon the side of the bulb against which the canal is coiled when retracted. He stated that the presence of the bipolar cells establishes the sensory character of these organs. He described the bulb as filled with vesicular or granular material, and tho no nuclei were discernible, regarded this as cytoplasm of granular cells in different stages of activity.

Looss (1902) in *Lophotaspis vallei* described two types of structures as occurring in the interstices between the muscular ridges of the ventral disc. Those around the periphery of the disc at the ends of the cross ridges he called "marginal bodies" and those at the intersections of the ridges he called "tentacles." The first he compared with the marginal organs of other aspidogastrid genera, and the tentacles differ only slightly in details of structure. He stated there was nothing in the structure

of the marginal bodies to warrant the former belief in their sensory character. Granules in the cavity he regarded as droplets of a secretion; and in the connective tissue dorsal to the cavity he described sac-like spaces with fine granular contents, and he found also nuclei but was uncertain whether they lay in the spaces or between them. The marginal bodies he regarded as glandular organs altho doubtful as to their exact function. He described the tentacles as having a spindle-shaped cavity with glandular apparatus around the inner end, and a canal leading from this blind end to the limiting membrane which formed the dorsal wall of the musculature of the adhesive disc. He considered these structures as adhesive or absorptive, but states that their physiological significance was doubtful.

Osborn (1904) in *C. insignis* described the marginal organs as consisting of three parts, the canal with its muscular wall, the cavity, and a dorsal fibrous part. The fibrous part he regarded "as a trunk of nerve fibers running at least to the muscles of the organ and perhaps partly sensory as well." The central cavity possessed "a lining of moderate thickness composed of cuticle outwardly but of nucleated epithelium on the inner side." This cavity he found empty or with one or more "concretionary objects." He says, "This indicates that secretion is going on the products being removed from time to time. I think the muscles described above may be used in discharging these products, the longitudinal fibers may act as dilators of the outlet, needed to enable such large objects to make their escape." Later he states, "I do not find in Cotylaspis any evidence of a glandular structure in the fibrous part, and do consider the bulbous part as epithelial and secretory."

The marginal organs apparently differ somewhat in structure in the different genera. Of all the authors, Looss alone seems to have morphological evidence for his conclusion that in Lophotaspis they are glandular in character. The statement of Osborn that in *Cotylaspis insignis* the bulb is partly lined with cuticula and partly with secretive epithelium, I regard as doubtful. Certainly in my sections of that species (Fig. 56) the bulb is lined with cuticula thruout. In the dorsal part of the cavity shown there are many small structures but they appear to be composed of the same material as the lining cavity. If they are cuticular, this would argue against the glandular character of the organ since in its functional activity the material would be swept out with the secretion instead of accumulating and forming such large objects as he shows in his figure. Furthermore it would be almost if not entirely impossible for such large bodies to pass thru the small canal which leads to the exterior. These "concretionary objects" are apparently the only basis for Osborn's claim that the organs are glandular since he stated that he

found no glandular structure in the fibrous part. Instead of supporting I believe that they are subversive to the idea of the glandular nature of the organ.

In my material the fibers which pass dorsad from the bulb are identical in appearance with the adjacent connective tissue and do not appear to be nervous. The muscular wall of the canal is I believe, used primarily in the eversion and retraction of the external part of the canal. In living specimens under observation the everted part of the marginal organ was about the size and shape of the thick-walled distal portion of the canal, and this is probably the only part protrusible. With this eversion, the base of the thick walled portion to which the nerve is distributed would be at the tip of the everted structure in a position to function in a sensory capacity.

Comparisons.—This is the third aspidocotylean described from turtles, the two previously reported forms being *Cotylaspis lenoiri* Poirier 1886, and *Lophotaspis vallei* Stossich 1899, both African species. Poirier described *C. lenoiri* from the intestine of *Tetrathyra vaillanti* from Senegal, and Looss (1902) reports it as occurring also in *Trionyx notilica* of the Nile. *Lophostaspis vallei* is parasitic in the stomach of *Thalassochelys corticata*. *Cotylaspis cokeri* is very different from Lophotaspis, but shows considerable resemblance to *C. lenoiri*. However, a comparison of the description of *C. lenoiri* with specimens of *C. insignis* and *C. cokeri* shows decided difference in the size and shape of the worms and of the adhesive disc, in the number of alveoli and marginal organs, in the sive of ovary and testis, of cirrus sac, and of eggs. The three forms agree in essential morphological features and fit the diagnosis of the genus Cotylaspis as given by Leidy, but are equally clearly good species in that genus.

CLASSIFICATION OF THE FAMILY

The last classification of the Aspidogastridae was made by Nickerson (1902). Since additions and changes have subsequently been made, further revision seems advisable. The present arrangement is largely based on the work of Nickerson and brings the classification to date. Present information supports the validity of the following genera.

I. Aspidogaster von Baer 1827. Type species, *A. conchicola* von Baer.

Oval adhesive disc, four rows of alveoli, marginal organs present, mouth subterminal, no oral sucker, one testis.

This genus contains *A. conchicola* which infests the pericardium and renal organs of various species of Unionidae in Europe and North America. It is also found in gastropods and in the immature condition in the intestine of Unionidae. Other species of this genus are *A. limacoides*

Diesing 1834 from the intestine of a fish (Leuciscus) in Europe, a form which Stafford (1896) and Kofoid (1899) suspect of being identical with *A. conchicola.* The species *A. macdonaldi* was placed in this genus by Monticelli (1892) and removed to Lophotaspis by Looss (1902). Linton (1905) described *A. ringens* from the intestine of *Micropognon undulatus* and *Trachinotus carolinus* at Beaufort, North Carolina. MacCallum and MacCallum (1913) gave a more complete description of *A. ringens* and described *A. kemostoma* n. sp., both from the intestine of *Trachinotus carolinus.*

II. Cotylaspis Leidy 1857. Type species, *C. insignis* Leidy.

Oval adhesive disc, three rows of alveoli, marginal organs present, mouth subterminal, no oral sucker, one testis.

This genus contains the species *C. insignis, C. lenoiri,* and *C. cokeri. C. lenoiri* was described by Poirier (1886) as a species of Aspidogaster. Monticelli (1892) created a new genus Platyaspis to contain Poirier's species, evidently overlooking the similarity between it and the form reported by Leidy. He declined to accept the genus Cotylaspis, suggesting that *C. insignis* was a species of Aspidogaster. Braun (1879-1893) ascribed the species to Aspidogaster. Kofoid (1899) established the validity of Leidy's genus but contended that the genus Platyaspis should be retained for Poirier's species. Nickerson (1902) argued that the differences between the African and American species are not of generic importance and suppressed the genus Platyaspis, making *Aspidogaster lenoiri* Poirier and *Platyaspis lenoiri* (Poir. 1886) Monticelli 1892, synonomous with *Cotylaspis lenoiri* Poir. *Cotylaspis insignis* occurs ectoparasitically in the mantle cavity of Unionidae in North America; *C. lenoiri* is from the intestine of *Tetrathyra vaillanti* of Africa; and *C. cokeri* is from the intestine of *Malacoclemys lesueurii* of North America.

III. Macraspis Olsson 1868. Type species, *M. elegans* Olsson.

A single row of confluent acetabula in adhesive organ, marginal organs present, mouth terminal, one testis.

The single species is parasitic in the gall bladder of *Chimaera monstrosa,* a fish from the coast of Europe.

IV. Stichocotyle Cunningham 1884. Type species, *S. nephropis* Cunningham.

A single row of more or less distinct acetabula, marginal organs lacking, mouth subterminal, oral sucker absent, two testes.

Cunningham's original description was of the larva and Monticelli (1892) declined to recognize its generic importance, thinking it might be a form of Macraspis. Odhner (1898) by discovering the adult and tracing the life history, established the genus. Adults live in the bile ducts of the liver of rays; larvae occur encysted in the wall of the intes-

tine of the larger marine Crustacea. Cunningham described it from the Norwegian lobster, Nephrops, and Nickerson (1895) reported it from the American lobster, *Homarus americanus.*

V. Cotylogaster Monticelli 1892. Type species, *C. michaelis* Monticelli.

Adhesive disc with three rows of alveoli, marginal organs present, mouth terminal, oral sucker present, two testes.

Two species have been described; *C. michaelis* occurs in the intestine of *Cantharus vulgarus,* a European fish, and *C. occidentalis* Nickerson 1899 is parasitic in the intestine of *Aplodinotus grunniens* of North America.

VI. Lophotaspis Looss 1902. Type species, *L. vallei* (Stossich) 1899.

Adhesive organ with four rows of alveoli, marginal organs present at all the intersections of the ridges of the adhesive disc, cirrus absent.

Loos in 1901 reported *L. adhaerens* as belonging to a new genus of the Aspidogastridae, but was not aware that Stossich two years before had described the same form as *Aspidogaster vallei.* Looss later (1902) described and figured the form under the name of *Lophotaspis vallei.* In the same paper he compared *A. macdonaldi* with *L. vallei* and placed the former species in the genus Lophotaspis. This trematode was reported but not named by Macdonald in 1878, and named by Monticelli (1892) as a species of Aspidogaster. Nickerson (1902) declared it to be an aspidogastrid, but different from all other known species, and predicted that a new genus would have to be erected for it when its structure was better known. Macdonald reported one hundred eighty extensile structures, like the tentacles of a snail, occurring at the margins and intersections of the ridges of the adhesive disc. Nothing is known of the internal structure. Looss in placing the form in the genus Lophotaspis stated: "Mit ihrer tentakeltragenden Bauchscheibe bildet die Art aber ganz zweifellos einen fremden Eindringling in der Gattung Aspidogaster, da dessen typischen Art jedenfalls solche Tentakel nicht besitzt. Gerade diesen auffallended Character aber teilt sie mit Lophotaspis; bin ich geneigt, *A. macdonaldi* Monticelli, trotzdem bei ihm die Genitalöffnung weiter rückwärts liegt als bei *Lophotaspis vallei,* aus dem genus Aspidogaster herauszunehmen and zu Lophotaspis zu stellen."

PARAMPHISTOMIDAE

HISTORICAL REVIEW OF THE FAMILY

The genus Amphistoma was created by Rudolphi (1801); concerning it Stiles and Hassall (1908) state, "Rudolphi deliberately renamed a previously validly named genus, namely Strigea Abildgaard, 1790, referring clearly to this fact both in 1801a, 50-51, and 1802b, 92. He makes but one combination (*Amphistoma subclavatum*), but since Amphistoma is clearly a new name proposed for an older one (Strigea), which Rud. changed on the alleged ground that it was inappropriate, Amphistoma should be suppressed in favor of Strigea and take the same species as type."

Fischoeder (1903) stated: "In Bezug auf den Namen Amphistomum will ich jedoch, wie schon gesehen (1901), nochmals darauf hinweisen, dass der Name Amphistoma von Rudolphi (1801) als neue Bezeichnung für die Gattung Strigea Abildg. 1790 eingeführtworden ist. Der Name Amphistoma kommt daher nach dem Prioritätsgesetz als synonym zu Strigea in Fortfall. Die ursprüngliche einzige und also auch typische Art der Gattung Strigea Abildg. 1790 (Amphistoma Rud. 1801) war *Planaria strigis* Goeze 1782 *Amphistoma macrocephalum* Rud. 1809 *Holostomum macrocephalum* Nitsch. 1819). Wenn daher der Name Strigea wieder zu Geltung wieder bebracht werden soll, so darf er nur für die heutige Gattung Holostomum weitergeführt werden, während die heutige Gattung Amphistomum einen anderen Namen erhalten muss. Ich habe in: Zool. Anz. 1900, V. 24, p. 367 den Namen Paramphistomum vorgeschlagen und, die Eintheilung nach dem Fehlen oder Vorhandensein der Pharyngealtaschen beibehaltend, in der Fam. Paramphistomidae Fischdr. (Amphistomidae Montic. 1888) die Unterfamilien Paramphistominae und Cladorchinae Fischdr. unterschieden. In diesen beiden Unterfamilien lassen sich die bekannten Formen unterbringen." The names Paramphistomum and Paraphistomidae have been accepted by Lühe, Looss, Odhner, and other writers and are used in this paper.

The paramphistomes of mammals were the first forms of this family discovered, and they have been the subjects of extensive study by Fischoeder (1903) and Stiles and Goldberger (1910); a number of species are known.

I have been unable to find any record of work done on the paramphistomes of fish between that of Diesing (1836) and MacCallum (1905). Daday (1907) described two species of Diplodiscus, two species of a new genus he called Microrchis, three species of a new genus named Pseudocladorchis, and added *Amphistoma oxycephalus* Dies. with two new species to the genus Chiorchis. He included a section on the anatomy and histology of the forms.

The only paramphistomes from amphibians are four species of Diplodiscus reported from frogs: *D. subclavatus* from the frogs of Europe, *D. temperatus* from those of North America, and *D. megalochrus* and *D. microchrus* from Australian frogs.

Information concerning paramphistomes of reptiles is very scanty. Braun (1901) lists three species from turtles: *Amphistoma grande* Diesing, *A. scleroporum* Creplin, and *A. sp.* Bellingham. Bellingham (1844) listed *Amphistoma sp.* from the intestine of *Chelonia imbricata* but gives no description, so this species should receive no further consideration. Braun (1901) supplemented the description of Creplin (1844) by a brief report of the single specimen of *A. scleroporum* from the museum at Greifswald, but the worm was sexually immature and consequently the observations were limited. *A. grande* was collected by Natterer from the intestine of five species of turtles in Brazil, but the description of Diesing is confined to the external appearance and the material may have comprised more than one species. One other species is known from turtles, a form described by Looss (1902) as *A. spinulosum* from the intestine of *Chelone mydas.* The description of Looss is very complete but because of the scarcity of known species and our limited knowledge of the group, at that time he refrained from any attempt at classification. He stated that the species is probably closely related to *A. scleroporum* and *A. grande.*

In addition to the description of the species, Looss (1902) discussed the question of the oral sucker and the pharynx in the group and compiling evidence from comparative anatomy and embryology, he argued that the anterior sucker of the amphistomes should be regarded as homologus to the oral sucker of the distomes. In this paper also he described the muscular thickening at the caudal end of the esophagus as a pharynx and described a peristaltic contraction of the organ from the anterior to the posterior end, altho in an earlier paper (1896) he had stated that the esophageal thickening of Gastrodiscus was not a true muscular pharynx. Concerning this latter structure, Odhner (1911) says, "Ich verwende diese Bezeichnung, weil es mir doch nicht so ganz sicher erscheint, dass es sich hier um ein dem gewöhnlichen Distomenpharynx homologes Organ handelt. Auch wenn es so wäre, könnte übrigens der

ziemlich verschiedene Bau einen besondern Namen rechtfertigen; der Oesophagus müsste aber dann konsequenterweise als Präpharynx bezeichnet werden." In his later paper Looss (1912) referred to this organ as an esophageal bulb.

The arrangement of the fibers in concentric lamellae and the function of the organ, acting as sphincter instead of a dilating pumping organ, argue against its homology with the pharynx of the distomes. These conditions I found myself in the two species of the new genus Alassostoma. However in the other of my new forms, *Zygocotyle ceratosa,* in stead of concentric muscle lamellae, the fibers at the sides of the lumen extend radially. A thickening of the esophageal musculature is described for Gastrodiscus, Homalogaster, Diplodiscus, Microrchis, Chiorchis, Schizamphistoma, Alassostoma, and Zygocotyle. In agreement with Looss (1912), the writer regards the tube leading from the oral sucker to the intestine at the esophagus and the muscular thickening of the wall of the esophagus as an esophageal bulb.

In this same paper Looss (1912) reinvestigated the species *Amphistoma scleroporum* and described its structure in detail. Discussing the taxonomy of the species he says, "Die Frage nach den Verwandtschaftlichen Bezeichnungen des *Amp. scleroporum* ist insofern leicht beantwortet, als seine enge Verwandtschaft zu *A. spinulosum,* auf die ich schon früher vermutungsweise hinwies (1902b, p. 437) jetzt offen zutage tritt. Ich würde nicht zögern, beide Arten in dieselbe Gattung einzureihen, wenn nicht gewisse, wenn auch kleine Differenzen im anatomischen Baue existierten die meiner Auffassung nach innerhalb von wirklich natürlichen Gattungen nicht vorkommen. Diese Differenzen bestehen, 1. in dem Fehlen des vor dem Mundsaugnapfe gelegenden starken Sphincters von *A. scleroporum* bei *A. spinulosum;* 2. der Reduction der Saugnapftaschen, die bei *A. spinulosum* deutlich, bei *A. scleroporum* nicht nach aussen hervortreten; 3. dem Fehlen der kleinen Seitenzweige an den vordersten Enden der Blasenschenkel von *A. scleroporum* bei *A. spinulosum;* 4. in dem etwas abweichenden Bau der Dotterstöcke (bei *A. scleroporum* in der Mitte fast zusammen and ohne eigentliche quere Dottergänge, bei *A. spinulosum* rein seitlich mit langen queren Dottergängen); 5. in dem etwas verschiedenen Verhalten der Lymphschläuche (ungemein reiche Verzweigung im Umkreise der Saugnäpfe bei *A. scleroporum,* kaum angedeutete Verzweigung bei *A. spinulosum*). Bin ich demnach auf Grunde dieser Unterschiede auch überzeugt, dass in den beiden Arten Repräsentanten je eines besondern Genus vorliegen, so genügt für meinen gegenwartigen Zweck doch die formelle Aufstellung der Gattung Schizamphistomum für *A. scleroporum,* in die ich *A. spinulosum* vorläufig provisorisch einbeziehe. Als die wesentlichen Charak-

tere dieser Gattung oder der Unterfamilie, zu der sie sich früher oder später auswachsen wird, betrachtet ich den Aufbau der Excretionblase aus zwei sehr langen, bis ins Kopfende einfachen, unter sich nicht verbundenen Schenkeln und den Aufbau des Lymphgefässsystemes aus jederseits drei in der Umgebung der Saugnäpfe verästelten Schläuchen."

He might well have added to his list of differences that in *S. spinulosum* there is a single loop of the excretory vesicle wound dorsally over the cecum of each side while in *S. scleroporum* there are eight loops winding irregularly around the cecum of each side. In the same article (p. 355) speaking of the excretory system in paramphistomes of mammals he says this system is situated deep in the body and in the larger groups is a stable and conservative organsystem. In a former paper Looss (1902 : 837) says, "Zwischen der Species einer natürlichen Gattung bestehen anatomische Unterschiede nicht; die Speciescharaktere werden dargestellt allein durch Differenzen in der Grösse des Körpers und der einzelnen Organe, Hand in Hand mit denen leichte Veränderungen ihrer Form, ihrer Lage und wenn sie reicher gegliedert oder in eine Anzahl von Theilstücken zerfallen sind, Aenderungen in der Zahl der Glieder resp. der Theilstücke gehen können." As a matter of fact, the argument of Looss in my opinion appears to show clearly that *S. scleroporum* and *S. spinulosum* are not members of the same genus; as indeed he has already suggested himself that in future researches a new genus will have to be created to contain *S. spinulosum.*

The single paramphistome reported from snakes was described by Cohn (1903) as *Amphistomum dolichocotyle,* and in his (1904) classification of the Diplodiscinae placed in the genus Catadiscus. It is from the intestine of *Herpetodryas fuscus.*

The only paramphistomes previously known from North America are *Amphistoma grande,* reported by Leidy (1888) from the intestine of the terrapin; two specimens from the small intestine of the muskrat which according to the same author, "appear to belong to *Amphistoma subtriquetrum"; Diplodiscus temperatus* Stafford long considered identical with *D. subclavatus* Dies.; and *Wardius zibethicus* Barker and East, from the cecum of *Fiber zibethicus.* The reports of Leidy contain no description except the length of the worms. Barker and East suspect that Leidy's specimens from the muskrat belong to their new genus and species *Wardius zibethicus;* and it is not unlikely that the specimens from the terrapin are specifically identical with those described here as *Alassostoma magnum* Stunkard 1916. Neither the description of Stafford nor that of Barker and East contains complete anatomical information. Stafford distinguished between the lymph and excretory systems. Barker and East make no mention of the lymph system; they

state that the oral sucker is wanting and describe the anterior sucker as the pharynx, notwithstanding the arguments of Pratt (1900), Looss (1902) and Stiles and Goldberger (1910) that the anterior sucker of the amphistomes is homologous with the oral sucker of the distomes..

The material of this family available for the present study consisted of representatives of two species from North American turtles, and another species from the duck, *Anas platyrhynchos*. A study of the literature showed that these forms could not be included in any previously described genera.

THE GENUS ALASSOSTOMA

A new genus Alassostoma is formed to include the two species from turtles. The genus is characterized by the presence of large oral evaginations which open independently into the oral sucker, an esophageal bulb composed of concentric muscle lamellae, a hermaphroditic duct, germ glands near the middle of the body in the median line, both testes anterior to the ovary, vitellaria consisting of small scattered follicles in the lateral, and posteriorly in median areas of the body, Laurer's canal opening in the mid-dorsal line anterior to the opening of the excretory vesicle. *Alassostoma magnum* is to be taken as type of the genus, and in it is included also the new species *A. parvum*.

The genus Alassostoma has the type of lymph and excretory systems present in the genus Schizamphistoma and designated by Looss as characteristic of the subfamily to which that genus belongs. Looss (1912) predicted that with the discovery of other forms it would be necessary to create a new subfamily to contain them, and at that time stated the subfamily characters. With the discovery of a second genus, so similar to Schizamphistoma that the two must be included in the same subfamily, the formal recognition of the new subfamily is necessary. Schizamphistoma Looss was designated as type and the name of the subfamily becomes Schizamphistominae. The subfamily contains the genera Schizamphistoma, including also *S. spinulosum* which as already indicated by Looss and discussed in this paper is type of a new genus, and the genus Alassostoma. The distinguishing characters of the subfamily as stated by Looss are two long excretory vesicles which extend singly to the anterior end of the body and a lymph system composed of three canals on either side of the body which run longitudinally and break up into many sinuses in the regions of the suckers.

Comparisons.—When one compares the species *A. magnum* and *A. parvum* with descriptions in the literature, they are seen to agree most closely with *Schizamphistomum scleroporum* and *S. spinulosum* Looss.

Mention has previously been made of the anatomical differences existing between these species and a statement ventured that such wide and fundamental differences should not be present in a natural genus. *A. magnum* agrees with *S. scleroporum* in general appearance and size, in type of excretory and lymph systems, character of vitellaria, and in general type of reproductive and alimentary organs; but *A. magnum* has large oral evaginations, which pockets are reduced and do not extend outside the sucker in *S. scleroporum,* and *A. magnum* lacks the preoral sphincter which is present in *S. scleroporum.* In *A. magnum* the uterus and cirrus sac open to the surface thru a common hermaphroditic duct; in *S. scleroporum* they open separately. Looss (1899 : 551) says one of the most important of generic characters is the structure of the copulatory organs. In *A. magnum* the testes are further posteriad and the ovary is situated one-fourth to one-third of the body length from the posterior end instead of at the level of the anterior margin of the acetabulum as is the case in *S. scleroporum.* In *S. scleroporum* the testes and ovary are widely separated and in *A. magnum* they are comparatively close together. These differences appear to be of sufficient importance to exclude the American species from the genus Schizamphistoma.

A. magnum agrees with *S. spinulosum* in the presence of oral evaginations and lack of preoral sphincter, but differs from it in the manner of the coiling of the excretory vesicles, in the presence of a common hermaphroditic duct and in the character of the vitellaria, as well as the relative positions of the testes and ovary. The morphological facts show differences too fundamental to permit the inclusion of both these species in a single genus.

Alassostoma parvum agrees with *A. magnum* in general morphological features, presence of oral evaginations,, lack of preoral sphincter, type of lymph and secretory systems, character of genital organs and ducts, also in relative position of testes and ovary. *A. parvum* therefore agrees with and differs from *S. scleroporum* and *S. spinulosum* in the same manner as *A. magnum.* That the two forms are not different developmental stages of the same species is shown by the great difference in the size of the worms and the relative differences in the size of suckers and genital organs. One of the species of *A. magnum* 10 mm. long is not sexually mature, while in the sectioned specimen of *A. parvum* which is less that 3 mm. long spermatoza were present in the testes and vas deferens. Further, ova were present in the oviduct, and the ootype and anterior part of the uterus were filled with spermatoza. Eggs were present in only one of the seven specimens of *A. magnum* and the absence of eggs in the three specimens of *A. parvum* does not signify that it is a young stage of *A. magnum. A. magnum* is large and has

small suckers and *A. parvum* is small and has relatively large suckers, and this feature suggested the name Alassostoma.

ALASSOSTOMA MAGNUM Stunkard 1916

[Figures 59 to 65]

The material of this species consists of one worm from *Pseudemys troosti* from Havana, Illinois; one from *P. elegans* from the same locality; two from *P. elegans* from Chicago, Illinois; and three specimens from an unknown turtle from Marshall, Missouri. The first four specimens were collected by the writer from the large intestine near its juncture with the small intestine, and the material from Marshall, Mo.,bears the label, "From cloaca of turtle."

In the preserved state the worms are 10 to 12 mm. in length, 3 to 5 mm. in breadth, and 1.5 to 2 mm. in thickness. One specimen studied in the living condition, measured 18 mm. in length when fully extended; preserved it is 11 mm. long, 3.8 mm. wide and 2 mm. thick. One fixed specimen 10 mm. long and 3 mm. wide is not sexually mature.

In the living state the worms are clear, hyaline, with the digestive ceca visible as brown lines. Their movements are very slow. In shape (Fig. 59) they are more or less oval, with the acetabulum forming a slight caudal projection. The acetabulum is slightly sub-terminal, circular or ovoid, usually wider near the anterior than the posterior end. The opening is necessarily relatively narrower than the sucker itself, in one specimen the opening is merely a slit, 1.4 mm. long, 0.38 mm. wide near the anterior end and posteriorly tapering to a point. In the largest specimens the acetabulum is 2.5 mm. long by 2 mm. wide, and in the smallest it is 2 mm. by 2 mm.

The cuticular covering of the body is unarmed, and measures 10 to 12μ in thickness. It is turned in at the openings of the excretory and reproductive systems and lines the digestive tract to the bifurcation. The dermo-muscular wall has the circular, longitudinal, and oblique layers well developed and inside the oblique layer there is an additional layer of longitudinal fibers (Fig. 60). Dorso-ventral fibers are scanty or lacking and the parenchyma of the body is very loose and vacuolated (Fig. 64).

Alimentary tract.—The oral sucker is terminal, spherical to ovoid in shape, usually longer in the antero-posterior axis and somewhat wider anteriorly than posteriorly. It is deeply set in the parenchyma of the body and measures 0.9 to 1.35 mm. in length and 0.6 to 0.9 mm. in width. Radial fibers pass from the external limiting membrane to the cuticula lining the sucker; in a cross section thru the sucker (Fig. 65), the inside

two-thirds of the outer half is a nuclear zone and all the nuclei are collected in this area. Half way between the nuclear zone and the lumen there is a narrow band of circular fibers. The oral evaginations arise at the caudal end of the oral sucker by two separate openings, one on either side, and extend dorsad and caudad. They are 0.35 to 0.6 mm. long, flattened dorso-ventrally, 0.15 to 0.2 mm. in width. These sacs are lined with cuticula and their wall is continuous with that of the oral sucker. Externally there is a layer of longitudinal fibers and inside this sets of annular fibers (Fig. 63). Oblique and radial fibers are occasionally seen but are very scanty.

The esophagus is 0.6 to 1.3 mm. in length; it is lined with cuticula and the wall contains external longitudinal and internal annular fibers. At the caudal end of the esophagus, just anterior to the bifurcation of the alimentary tract, there is a prominent esophageal bulb. It varies from 0.65 to 0.95 mm. in length and from 0.33 to 0.5 mm. in width; it is formed by a thickening of the annular fibers of the wall of the esophagus. A cross section is represented in Figure 60 and shows the eighteen concentric lamellae of muscles. No nuclei are present in these annular muscles. Both the oral evaginations and the esophagus are surrounded by clusters of deeply staining cells (Fig. 63). Looss (1896) described similar cells in Gastrodiscus and believed they secrete the lining of the esophagus. The ceca are flattened laterally and are of very unequal caliber, small lateral evaginations occur on opposite sides at the same level recalling the condition in some of the Turbellaria. The diverticula extend almost to the acetablum, about 0.37 mm. intervening. They have a muscular coat consisting of external annular and internal longitudinal fibers and an epithelial lining of columnar cells which show faint longitudinal striations (Fig. 62).

Male Reproductive Organs.—The testes are slightly lobed, oval, longer in the transverse diameter, and vary in size from 0.27 by 0.35 mm. to 0.45 by 0.9 mm. They are situated one behind the other or in contracted specimens slightly on opposite sides of the median line. They are approximately the same size in any one specimen and are separated by about the length of one of the testes, tho in contracted specimens they may lie closer together. The vasa efferentia arise from the dorsal anterior margins, the duct from the posterior testis on the left and the duct from the anterior testis on the right side of the body. They pass dorsad and cephalad, and 0.4 to 0.5 mm. caudad of the bifurcation of the digestive tract they unite to form a much coiled seminal vesicle, which near the pore passes into a small, poorly developed cirrus sac. In sectioned individuals it could be seen that the seminal vesicle was filled with spermatoza. In one specimen the coils of the vesicle extend thru twenty

cross sections each 15μ in thickness, and the tube is so coiled that in a section of the worm there are ten or fifteen sections of the vesicle. In another individual cut in frontal sections the seminal vesicle extends anteroposteriorly thru 0.57 mm. The prostate gland is enclosed by the cirrus sac and fills the entire region between the wall and the central canal. The cells are more numerous in the posterior part of the sac, gradually becoming fewer in the anterior region. The sac is approximately 0.37 mm. long and 0.185 mm. in diameter. It is dorsal on the right side of the body, and the terminal end of the uterus is ventral on the left side of the body.

Female Reproductive Organs.—The ovary is spherical or oval, 0.275 to 0.35 mm. in length and 0.33 to 0.57 mm. in width, in or near the median line, about the width of the caudal testis behind the latter. The oviduct is very small and arises from the dorsal margin of the ovary (Fig. 61). After a coil posteriad Laurer's canal is given off and passes in a winding course to the dorsal surface. There is no receptaculum seminis. Just after the origin of Laurer's canal, the oviduct passes into Mehlis' gland, where the vitelline duct is received. There is no vitelline receptacle in either of the sectioned worms, but the right and left ducts are very large. They meet in the median line posterior and ventral to Mehlis' gland, and a duct passes to the ootype. The uterus coils anteriad, either between or around the testes and opens thru the hermaphroditic duct to the genital pore.

The genital pore is in the median line ventral to the esophageal bulb, and there is a small genital sinus. The cirrus sac and metratermal portion of the uterus open to the exterior thru a common hermaphroditic duct (Fig. 60).

The vitellaria consist of small irregularly shaped follicles, lying almost entirely in the ventral half of the body and extending from the region of the cephalic testis to the caudal ends of the ceca. Anteriorly they are extracecal, but posteriorly they extend into the intracecal area; near the ends of the ceca about half of the follicles are between the diverticula.

Eggs were present in only one specimen. Here there were three; they measured 0.1 by 0.13 mm.

Lymph System.—This system consists of three canals passing longitudinally on either side of the body, one lateral and two mesal of each cecum. Of the median pair, one is dorsal and the other ventral (Fig. 59). These canals are not straight but wind about and give off branches at various points. These branches subdivide in turn and at the ends the main trunk breaks up into numerous smaller branches so that the entire body is penetrated by ramifications of this system. The ceca, the genital

organs, and the suckers are especially well supplied with lymph sinuses.

Excretory System.—The excretory pore is in the median line on the dorsal surface, near the posterior end of the body, and the median terminal vesicle extends internally and anteriorly. It gives off a branch to either side and these branches of the collecting vesicle pass anteriad, winding about the cecum of either side in many loops or coils. In sections (Fig. 64) the tube may appear on either side, above, or below the cecum; in a single section it may be cut in two or three places or a loop may pass half to two-thirds of the way around the cecum. No connections between the collecting ducts of the two sides could be seen, and they were traced to the region of the oral sucker.

ALASSOSTOMA PARVUM Stunkard 1916

[Figures 66 to 71]

Three individuals of this species were collected from the cloaca of a single specimen of *Chelydra serpentina* from Urbana, Illinois. One was retained as an alcoholic specimen, one was stained and mounted as a toto preparation, and the third was cut into cross sections.

The worms (Fig. 66) are thick with almost parallel sides, rounded at the posterior end and tapering slightly anteriorly. Just in front of the acetabulum the body narrows slightly and then widens posteriorly due to the presence of two lateral prominences or evaginations, one on either side at the level of the anterior part of the acetabulum. The worms are 2.8 to 3 mm. long and 0.78 to 0.08 mm. wide, the points of greatest width are at the level of the testes and thru the posterior lateral prominences. The sectioned worm is 0.8 mm. in width and 0.54 mm. in thickness. The acetabulum is subterminal, oval, 0.8 mm. in length and 0.7 mm. in width in the toto preparation. The inside measurements of the same sucker are 0.56 mm. in length by 0.4 mm. in width and the opening is 0.45 mm. in length and 0.21 mm. in greatest width.

Alimentary Tract.—The oral sucker is terminal, ovoid, 0.46 mm. long by 0.37 mm. wide, and in the sectioned worm 0.32 mm. in depth. In the mounted specimen the sucker is widest posteriorly, and from the posterior dorsal part on either side there is an oral evagination. These arise separately and are 0.055 mm. long. Among the fibers of the oral sucker there are many nuclei; they are situated in the peripheral half of the sucker and are confined to the central two-thirds of the external half. There are also among the muscle fibers glandular cells with ducts to the lumen of the sucker. The esophagus is somewhat coiled but extends thru 0.2 mm. and is surrounded by large deeply staining gland cells. The posterior part is enlarged by the thickening of the annular muscles of the wall which forms the esophageal bulb (Fig. 70). This

structure comprises twelve concentric rings or lamellae of muscles. It is 0.2 mm. long by 0.14 mm. wide in the toto specimen and 0.314 mm. in depth in the sectioned individual. The diverticula extend posteriad almost to the cephalic margin of the acetabulum. In sections they are oval, and flattened laterally. In the intestine of the sectioned worm there are masses of small nuclei, possibly from the epithelial lining of the cloaca of the host.

Male Reproductive Organs.—The testes are oval, in the toto specimen they are 0.17 mm. long by 0.17 mm. wide, and in the sectioned worm 0.17 mm. wide by 0.29 mm. thick. They are situated one in front of the other in the median line and in the ventral part of the body. They are close together, separated only by a thin fibrous sheet. The vasa efferentia arise at the dorsal margins of the testes; the duct from the caudal testis pass anteriad and anterior to the cephalic testis unites with the duct from this latter testis. The vas deferens immediately expands into a long much-coiled seminal vesicle which passes anteriad and into the cirrus sac (Fig. 69). Inside the cirrus sac the tube continues in large coils; the terminal part is surrounded by the cells of the prostate gland and opens to the surface thru a short hermaphroditic duct. There is a small genital papilla (Fig. 71).

Female Reproductive Organs.—The ovary is oval; in the toto specimen it is 0.098 mm. long and 0.088 mm. wide, and in the sectioned worm it is 0.95 mm. wide and 0.134 mm. thick. It is median in position and situated midway between anterior and posterior ends of the body. The oviduct arises at the dorsal posterior margin and passes dorsad and posteriad into Mehlis' gland. This gland is large and well developed. Here Laurer's canal is given off and passes in short coils to the dorsal surface. Just after the origin of Laurer's canal a short common vitelline duct opens into the ootype and the oviduct passes ventrad. It expands to form the initial part of the uterus, turns anteriad, and is filled with masses of spermatoza. The expanded portion of the uterus extends anteriad half the distance to the caudal testis and then the tube contracts, passes dorsad and in a winding course over the testes. Anterior to the testes it turns ventrad and enters the hermaphroditic duct on the posterior ventral side. The vitellaria extend from the region of the testes to the caudal ends of the digestive ceca and consist of scattered lobes, mostly ventral in position. Anteriorly they are extracecal but behind the ovary they are intracecal as well.

No eggs were present in any of the specimens.

The genital pore is in the midventral line, just posteror to the bifurcation of the alimentary tract. There is a genital sinus but no genital sucker.

Lymph System.—The lymph system is similar to that described for *A. magnum* and consists of the three longitudinal canals on either side of the body, one canal lateral to each cecum and a pair, one dorsal and the other ventral, mesal to the diverticulum of either side. The secondary branchings could not be traced but lymph sinuses are present in sections in all parts of the body, and those around the acetabulum are shown in Figure 68.

Excretory System.—The excretory pore is median, dorsal, at the level of the cephalic margin of the acetabulum. A short median vesicle passes ventrad and anteriad and divides into two collecting vesicles as in *A. magnum.* These pass ventrad and posteriad, one on either side, loop around the caudal ends of the diverticula, and then turn anteriad, winding around the ceca in many irregular coils so that in sections they appear lateral, mesal, ventral or dorsal to the intestine; often the tube is cut two or three times in the same section or a single section may show a coil encircling the cecum for half or more of its circumference (Fig. 67). Anterior to the bifurcation of the alimentary tract the ducts continue in the lateral areas of the body and can be traced almost to the oral sucker.

THE GENUS ZYGOCOTYLE

The only known form with which the paramphistomes from the duck can be compared is *Amphistoma lunatum.* This species was described by Diesing (1836); the material had been collected by Natterer in Brazil, South America, from the cecum of *Anas melanotus, A. ipecutiri, A. moschata, Himantopus wilsonii,* and also from the cecum of *Cervus dichotomus.* Fishoeder secured the original specimens from the Vienna museum and (1903) gave a more extended description of the form, altho his study was restricted to the examination of toto preparations. He stated that the citation of *Cervus dichotomus* as a host of this form is probably an error, and the same suspicion had been mentioned by Diesing (1850). It is at once apparent that the present species is very similar to *A. lunatum.* Both are parasites of American ducks, and are the only paramphistomes at present known from avian hosts. They are nearly equal in size, are similar in shape, have a subterminal oral sucker, reproductive systems that compare very closely, digestive tracts similar in character, and acetabula of the same form consisting of an anterior section and a posterior overhanging lip which terminates on either side in a small cone-like projection.

Amphistoma lunatum has been placed as an appendix to every classification of the paramphistomes that has ever been attempted. With the discovery of a form so similar, the two must belong together and a new genus is proposed to contain the two species. The peculiar divided

condition of the acetabulum suggested the name Zygocotyle as appropriate for this genus. *Zygocotyle ceratosa* has been designated as type and in the genus is included also the species *Amphistoma lunatum*.

As diagnostic characters of the genus Zygocotyle may be mentioned the subterminal oral sucker, the posterior sucker divided or provided with caudal overhanging lip, absence of cirrus sac and separate openings of the male and female ducts. Others will undoubtedly appear when the character of the excretory and lymph systems are known. The genus Zygocotyle differs from all other known genera of the Paramphistomidae in the ventral position of the oral sucker and the peculiar character of the acetabulum. It differs from the Gastrodiscinae in the shape of body and absence of ventral papillae, and from the Gastrothylacinae in the absence of the ventral pouch. In the lobed testes and absence of cirrus sac it agrees with the Paramphistominae, but the oral evaginations exclude it from that group. The absence of cirrus sac and the lobed form of the testes will not permit its inclusion with the Cladorchinae. The characters of the Diplodiscinae are so poorly defined that a comparison is unsatisfactory; in this group however, a cirrus sac is present and both suckers are terminal. As none of the existing subfamilies will include the genus, a new subfamily will probably have to be made to contain it. Since the present classification of the Paramphistomidae is somewhat uncertain, and the structure of the excretory and lymph systems of this genus are as yet unknown, no further attempt at classification of the group is made at this time.

ZYGOCOTYLE CERATOSA Stunkard 1916

[Figures 72 to 79]

The material of this species consists of eight specimens from the intestine of *Anas platyrhynchos* from Rock County, Nebraska. The intestine of the duck had been cut open in places and together with its contents preserved in formalin. The fixation of the parasites is so poor that the excretory and lymph system can not be traced, altho remnants of both appear in sections.

These worms (Fig. 72) vary in length from 3 to 6 mm. and in width from 1.45 to 2.14 mm. In dorsal or ventral aspect they are elongate oval in shape with the acetabulum forming a small terminal projection. The cross section is a flattened oval and toward the ends of the body becomes more circular. The acetabulum is subterminal and consists of two parts (Fig. 77), an anterior part extending dorsally and anteriorly into the body and a posterior overhanging lip which terminates on either side in a little horn or conical projection 0.12 to 0.2 mm. in length. The

cephalic part extends anteriad about 0.46 mm. from the anterior margin of the opening of the sucker. The opening of the acetabulum is oval approximately 1.1 mm. in length and 0.74 mm. in diameter. The septum or partition which divides the sucker extends almost to the opening and appears to separate an anterior circular part from the remaining portion but there is a single oval opening of the acetabulum.

The cuticula is unarmed, slightly thicker on the dorsal surface. On the ventral surface it is about 12μ in thickness and reaches 30μ in thickness on the dorsal surface. It is not homogeneous, but is traversed by fine crinkled lines extending from internal to external surfaces, which give it a reticulated appearance. The entire dorsal surface of the body is underlaid with large gland cells filled with a substance staining deeply with haematoxylin; and their ducts lead to the dorsal surface. The contents of the gland cells and their ducts have the same appearance and staining reaction as the cuticula of the external surface. The dermo-muscular sac consists of the usual circular, longitudinal, and oblique layers, the circular layer is next to the cuticula. From the body wall there are many large dorso-ventral muscle strands extending thru the body.

Alimentary Tract.—The oral sucker is subterminal, circular or slightly oval in shape, 0.37 to 0.53 mm. in diameter. The oral evaginations are 0.15 to 0.22 mm. in length and 0.07 to 0.1 mm. broad; they branch one on either side from a common sinus (Fig. 74) which opens into the dorsal side of the posterior part of the oral sucker. The esophagus leads from the oral sucker to the intestine; it is 0.05 to 0.37 mm. in length and is surrounded by a layer of deeply staining cells. Its caudal portion is surrounded by an esophageal bulb. This structure is oval, 0.2 to 0.45 mm. in length, 0.18 to 0.23 mm. in width, and 0.35 mm. in thickness in the specimen cut in cross sections. It is situated obliquely in the body, the anterior end is ventral and the posterior end more dorsal in position. The muscles are not arranged in concentric lamellae as in the previously described paramphistomes; there is a capsule of external longitudinal fibers and the body of the organ is composed of fibers extending on the sides from the central canal to the external capsule and above and below the canal the fibers extend across from the lateral walls of the bulb (Fig. 73). The alimentary tract is lined with cuticula to the bifurcation. The ceca are flattened laterally and the lateral walls are sinuous giving them a very irregular appearance. They have a muscular wall composed of outer circular and inner longitudinal fibers and extend almost to the opening of the acetabulum, about 0.1 to 0.15 mm. intervening. They terminate just caudad of the excretory pore.

Male Reproductive Organs.—The testes lie one behind the other in

the median line, the caudal testis is almost in the center of the body, and the cephalic testis is about 0.2 mm. in front of it. They are about the same size, lobulated, oval, crosswise of the body, almost touching the cecum of either side. They are ventral in position, almost touching the ventral body wall and not extending far into the dorsal half of the worm. They vary in size from 0.2 by 0.3 mm. in the smallest to 0.55 by 0.78 mm. in the largest specimen. The vasa efferentia arise from the anterior dorsal margins, the right tube from the anterior and the left tube from the posterior testis. Near the genital pore they unite and form a much coiled seminal vesicle which has a thickened muscular wall. This structure extends thru twenty-five cross sections cut 10μ thick. The terminal part that leads ventrad to the genital pore is expanded, the walls are thinner, and this part is surrounded by the cells of prostate gland. A cirrus sac is absent, the male and female tubes open to the exterior independently at the apex of a slight ventral prominence. The opening of the male duct is immediately anterior to that of the female (Fig. 78).

Female Reproductive Organs.—The ovary is oval, lobulated, crosswise of the body, about the shorter diameter of the testis behind that organ. In the smallest specimens it is 0.2 by 0.33 mm. and in the largest 0.33 by 0.52 mm. The oviduct arises at the dorsal margin as a very small tube and passes dorsad where Laurer's canal is given off. This canal winds in short curves to the dorsal surface, opening anterior to the excretory pore (Fig. 79). After the origin of Laurer's canal the oviduct passes posteriad and ventrad into Mehlis' gland where a short common vitelline duct is received. The uterus then coils irregularly in close folds to the genital pore. The uterine coils are largely in the dorsal part of the worm altho they may extend into the ventral portion and coil around the testes. Laterally the coils of the uterus are limited by the ceca. The terminal part has a slight thickening of the wall but not a distinct delimited metraterm. The vitellaria are well developed, large follicles extending in the extracecal areas from the level of the posterior edge of the oral sucker to the anterior margin of the opening of the acetabulum. They are limited medially by the ceca and laterally extend almost to the body wall. They are more ventral than dorsal in position.

Eggs are present in large numbers. In size they average 0.14 by 0.083 mm.

Comparison.—*Zygocotyle ceratosa* agrees with *Z. lunata* in length, width, and size of oral sucker, but in the former species the oral evaginations are smaller, the esophagus is much shorter, the testes and ovary are oval and lobed instead of circular, and the ceca do not extend to the opening of the acetabulum. In *Z. ceratosa* the acetabulum is nearer the ovary, and the vitellaria are entirely extracecal while in *Z. lunata* they extend between the ceca.

CLASSIFICATION OF THE FAMILY

Our present classification of the Paramphistomidae is largely the result of the work of Monticelli, Otto, Fischoeder, Cohn, Daday, Stiles and Goldberger, Looss, and Odhner.

The first division of the group was made by Monticelli (1892) when he separated Gastrodiscus from the rest and created the subfamily Gastrodiscinae. Fischoeder in a series of papers described several species from mammals, and formulated (1903) the second scheme of classification. He created two subfamilies: Paramphistominae in which the testes are lobed, and paired oral evaginations and cirrus sac are absent; and Cladorchinae characterized by branched testes and the presence of paired oral evaginations and cirrus sac. Recent additions to our knowledge of the family have, however, rendered it difficult to use these distinctions satisfactorily. Cohn (1904) created the subfamily Diplodiscinae to contain the genera Diplodiscus, Opisthodiscus, and Catadiscus. He characterized the subfamily as follows: "Amphistomiden von gedrungener, konischer Form und runden Querschnitt. Mundsaugnapf gut ausgebildet, mit zwei retrodorsal Taschen. Ein grosser Endsaugnapf, über welchem dorsal der Excretionsporus liegt. Mundöffnung terminal, Darmschenkel bis zu Endsaugnapf reichend, relativ sehr breit. Leben im Enddarm von Amphibien und Reptilien." The characterization is inadequate, since the anatomical features are shared by almost half the members of the family, and obviously further study of this group is necessary to establish its validity and determine its true diagnostic features.

Stiles and Goldberger (1910) proposed a new classification of the group. They created a new superfamily Paramphistomoidea to contain the forms previously classed as amphistomes. They removed Gastrodiscus Leuck., and Homalogaster Poir. from Fischoeder's subfamily Cladorchinae and created a new family Gastrodiscidae to contain these genera. They created another new family Gastrothylacidae to contain the general Gastrothylax, Wellmanius, Carmycrius, and Fischoederius. The family Paramphistomidae and the two cited above comprise the three families in the superfamily Paramphistomoidea. Stiles and Goldberger also created a new subfamily Stephanopharynginae to contain the genus Stephanopharynx, and added the new genus Cotylophoron to the subfamily Paramphistominae. They recognize further the subfamily Diplodiscinae Cohn and list the four subfamilies Paramphistominae, Cladorchinae, Diplodiscinae, and Stephanopharynginae in the family Paramphistomidae. They placed Balanorchis in the subfamily Cladorchinae notwithstanding Fischoeder's statement that such an arrangement could not be considered.

Braun (1911) reviewing the article, objects to the rank of superfamily for the paramphistomes and says placing them on an equality of rank with the Fascioloidea is not justifiable.

The work of Stiles and Goldberger is criticized at the hands of Odhner (1911) as follows: "Dies alles zeigt nun evident, wie wenig Verstandnis die betreffenden Autoren für die moderne natürliche Digenensystematik haben. . . . . Mir scheint nun diese "Argumentation" ebenso wie viel anders (die neue topographische Terminologie) in derselben arbeit sehr "unwise" zu sein. . . . . die Amphistomen entsprechen im systematischen Range einer einzelnen Distomenfamilie und nicht, wie Stiles and Goldberger gelaubt haben, der Summe sämtlicher dieser Familien."

Looss (1912) also gives a critical review of the paper: Die Charakterisierung der Arten, Gattungen usw. baut sich auf, einerseits auf eine pedantisch ins einzelne gehende Analyse und Beschreibung der Körperform und der Topographie von Darm und Genitalapparat, anderseits auf eine konsequente Ignorierung der beiden Tatsachen, dass die Tiere, als Organismen, innerhalb gewisser Grenzen natürlich variieren, und dass Körperform sowohl wie Topographie der Organs mit dem Wachstum gesetzmässige, mit der Kontraktion a priori nicht bestimmbare Veränderungen erleiden. Der Aufbau von Lymph—und Excretionsapparat bleibt völlig unberücksichtigt. Dass die Amphistomen ein "Lymphgefässsystem" überhaupt besitzen, scheint den Autoren unbekannt zu sein."

The classification of Stiles and Goldberger as pointed out by other authors is based on superficial characters and the elevation in rank of the family and groups within the family is in most cases unwarranted. However, the subfamily Gastrothylacinae of these authors appears to be clearly distinguished by the presence of the large ventral pouch, and in my opinion should be retained.

Looss (1912) considers the lymph and excretory systems of major importance in classification. As characters of the new subfamily Schizamphistominae he mentioned the type of lymph and excretory systems. Since the lymph system has not yet been described in other subfamilies, the former diagnoses based on body form, types of digestive and reproductive systems, presence of ventral pouch, etc., must be retained for the present. Moreover, since so many of the forms are incompletely described, and considerable difference of opinion exists in regard to the taxonomic value of the different features, the classification of the group is still uncertain. As Looss (1912) says, "Jeder Klassifikationversuch, der der bau von Excretions—und Lymphgefässsystem ausser acht lässt, mag sich wohl einen Klassifikationsversuch nennen, kann aber niemals

Anspruch darauf erheben, als naturlicher oder (was dasselbe ist) wissenschaftlicher Klassifikationsversuch anerkannt zu werden.'' In the same article he states that for many years he has been engaged in preparing a revision of the amphistomes but has not yet completed the work which will present a classification based on the structure of the lymph and excretory systems and the copulatory apparatus.

The only arrangements of the genera of the family that have been made heretofore are those of Fishoeder and of Stiles and Goldberger. The classification of Fischoeder does not appear adequate and that of Stiles and Goldberger is far from satisfactory, but for sake of completeness both are appended in outline.

Classification of Fischoeder (1903)

Paramphistomidae
- Paramphistominae
  - Paramphistomum
  - Gastrothylax
  - Stephanopharynx
    - Species inquirendae, *A. gigantocotyle*, *A. explanatum*
- Cladorchinae
  - Cladorchis
  - Gastrodiscus
  - Homalogaster
  - Diplodiscus
  - Chiorchis
    - Species inquirendae; *A. hawkesi, A. collinsi, A. ornatum, A. papillatum, A. tuberculatum, A. emarginatum,* and *A lunatum.*
- (Subfamily nov.)
  - Balanorchis

Classification of Stiles and Goldberger (1910)

Paramphistomoidae
- Gastrodiscidae
  - Gastrodiscus
  - Homalogaster
- Gastrothylacidae
  - Gastrothylacinae
    - Gastrothylax
    - Wellmanius
    - Carmyerius
    - Fischoederius

Paramphistomidae
Paramphistominae
Paramphistomum
Cotylophoron
Cladorchinae
Cladorchis
Taxorchis
Chiorchis
Microrchis
Pseudocladorchis
Pseudodiscus
Balanorchis
Watsonius
Pfenderius
Diplodiscinae
Diplodiscus
Catadiscus
Opisthodiscus
Stephanopharynginae
Stephanopharynx

As a result of my studies on this family, certain data have been added and some doubtful points cleared up. The discovery of the two species of the new genus Alassostoma and the demonstration of their position as members of a new genus in the subfamily Schizamphistominae Looss establishes that group. The description of the new genus and species *Zygocotyle ceratosa* throws considerable light on the previously isolated and obscure species *A. lunatum* Dies. In conclusion I present a tentative revision of the paramphistomes. In the main it is my interpretation of the status of the group and its subdivisions. The new genera of Stiles and Goldberger are included without comment altho certain authors do not recognize their validity. I have had no opportunity to work on this material and consequently any judgment on my part must appear unwarranted. Because of the scarcity of known forms and the incompleteness of most of the descriptions it is impossible to present a final classification. The following arrangement is provisional and likely to be replaced whenever a natural system can be formulated for the family.

Paramphistomidae Fischoeder 1901
Gastrodiscinae Monticelli 1892
Gastrodiscus
Homalogaster
Paramphistominae Fischoeder 1901

Paramphistomum
Stephanopharynx
Cotylophoron
Cladorchinae Fischoeder 1901
Cladorchis
Taxorchis
Chiorchis
Pseudodiscus
Microrchis
Pseudocladorchis
Watsonius
Pfenderius
Diplodiscinae Cohn 1904
Diplodiscus
Opisthodiscus
Catadiscus
Gastrothylacinae Stiles and Goldberger 1910
Gastrothylax
Wellmanius
Carmyerius
Fischoederius
Schizamphistominae Looss 1912
Schizamphistomum
(*Gen. nov.*) *spinulosum*
Alassostoma
Genera of uncertain position
————(new subfamily) Fischoeder 1903
Balanorchis
————(new subfamily) see text p. 71
Zygocotyle

RELATION OF THE FAMILIES TO THE ORDER

The trematodes are generally regarded as descended from a turbellarian-like ancestor which possessed a posterior sucker. With the assumption of the parasitic habit adaptations began in various directions. The ectoparasitic forms retained many of their former characters while the added protection and food supply afforded those specializing toward endoparasitic existence provided for perpetuation and distribution of the species thru the excessive development of the reproductive apparatus. The development of the ectoparasitic forms is simple and direct while that of most if not all endoparasites has been complicated by the interpolation of one or even more secondary or intermediate hosts.

The differences in type of adhesive apparatus may in a general way be explained thru differences in habit. The oral sucker has developed thru continued adhesion by the anterior end in maintaining position, in locomotion, and in securing food. In the Gasterostomidae the mouth is on the ventral surface and an independent anterior sucker is developed, altho this is undoubtedly a secondary feature, as in the cercariae of these forms there is a single anterior oral sucker. In response to the constant necessity for strong adhesion the ectoparasitic species have developed accessory posterior organs of attachment, while in most of the endoparasitic forms the acetabulum has migrated anteriad or disappeared entirely.

The general classification of Monticelli, which is followed in this paper, is based primarily on the character of the adhesive apparatus. In the Heterocotylea the posterior sucker has been replaced by a disc which bears suckers and hooks; in the Aspidocotylea the acetabulum has become specialized into a multiloculate adhesive organ; and in the Malacocotylea the acetabulum may be retained in its primitive terminal position, or it may have migrated anteriorly, in certain cases being reduced and in others disappearing entirely. In the young individuals of many forms in each of the three groups there is a single posterior sucker and this fact adds weight to the theory that the present groups are descended from a primitive form with a simple posterior sucker. In the young stages of all the Aspidogastridae there is a simple posterior sucker and the worm closely resembles a young distome. In the early stages of the Heterocotylea the reversion to the ancestral conditions is not so complete, and specialization in this group shows clearly that it is widely separated

from the other two suborders which thru the presence of similar young forms appear to be more closely related.

The morphological structure and direct development of the Polystomidae at once places them with the Heterocotylea. In the adoption of an endoparasitic mode of life, however, thy show a distinct departure from the other members of the suborder. The present study of the Polystomidae has emphasized the unusual morphological variation and wide geographic distribution which exists in the family. This may mean either that the family is very old and has been subjected to conditions producing wide variation, or that the group really lacks family entity and consists of various heterocotylean forms which have specialized in the direction of an endoparasitic habit and that the morphological resemblance is cenogenetic.

Pratt (1908) reviews the literature and arguments for convergent development which are based on trematode morphology. Johnston (1914) argues for divergence as the true explanation of the variation of the species of Pneumoeneces, Gorgoderinae, Brachycoelinae, etc., and believes that the elucidation of trematode phylogeny may be sought in the study of the relationships between the distribution of trematode parasites and the distribution of their hosts. No doubt the likenesses and differences in the structure of present species are the result of both convergence and divergence; yet it seems that the distributional factor emphasized by Johnston is not of major importance. Parasitic distribution could precede the distribution of the primary and secondary hosts only in case the parasites changed to new primary or secondary hosts. But today more than one species may serve as primary or secondary host; the parasite is probably in a restricted degree able to adapt its life history physiologically so other species may serve as hosts, and primitively this adaptability may have been greater than now. The distribution of the parasites certainly depends to a large extent on the distribution of the primary host, and to a less extent on the distribution of the secondary host, but the presence of two similar parasites in the same region does not prove that their hosts had primitively the same or different parasites. The life history of the trematodes is so imperfectly known that at present no final decision can be made on this basis.

The wide variation in structure of the members of the genus Polystoma can not be adequately explained thru migration, or thru differences in the age of the parasite, type of host, or location in the host. In the genus so far as is known, the long uterus containing many eggs is confined to species infesting the urinary bladder of amphibian hosts of the Old World. However in respect to other characters, e. g., the shape of the caudal disc and absence of great hooks, these amphibian forms of

the Eastern hemisphere disagree with each other and agree with forms parasitic in the urinary bladder and oral cavity of North American turtles. The turtle parasites have a very similar structure, whether parasitic in the urinary bladder or in the pharyngeal cavity. Furthermore, if the observations of Zeller are correct and the individuals of *P. integerrimum* becoming mature on the gills of tadpoles lack external vaginae and have a spherical testis and a single egg in the uterus, one is entirely at a loss to explain the variation existing in the genus.

In the Aspidogastridae the young individuals have an oral sucker and a small posterior acetabulum without dividing ridges, and very closely resemble young distomes. The mode of infection is almost entirely unknown, and this offers a promising field for investigation. The discovery of the sexual form of Stichocotyle by Odhner (1898) establishes the fact that at least one species of the Aspidogastridae has an intermediate host. Nickerson (1895) observes, "Owing to the well known tendency of fresh water conditions to obliterate larval life, it may well be that Aspidogaster has secondarily lost a more or less complicated series of changes, which have been retained by its relatives inhabiting salt water." The presence within the family of both direct and indirect development, together with other characters common to both the Heterocotylea and Malacocotylea designate it as an intermediate group. The morphological structure is similar to that of the Malacocotylea while the manner of development is similar to that of the Heterocotylea. Whether the Aspidogastridae are primitive forms or are secondarily degenerate is as yet undecided. The simple and archaic character of the intestine, the eye spots, the direct development and the ectoparasitic habit as it occurs in the family, together with the parasitic infection of molluscs by adult forms strongly suggests a very primitive and ancient group. It is probable that complete evidence concerning the structure and life history of this family would go a long way toward solving the problem of whether the invertebrate or the vertebrate is the original host and the attendant problem of the origin of double hosts.

The Paramphistomidae appear to be a primitive family of the Malacocotylea that have retained the original caudal sucker, altho certain species show specializations of the organ from the simple spherical type. Considerable light is thrown on the relationships of the Malacocotylea by the recent work of Odhner on a natural system for the digenetic trematodes. He strongly advocates the view that the monostomes are a group which have no family entity, and consist of individual forms derived from various distome groups which have alike lost the acetabulum. Pointing out close and fundamental agreement in internal

structure he argues that the monostome family Angiodictyidae is really a subfamily of the Paramphistomidae. He shows essential morphological agreement between *Distoma quadrangulum* Daday and the fish amphistomes. His examination of the original specimen of Aspidocotyle confirms the statement of Braun (1879-1893) that this form belongs to the amphistomes, altho its relation to the other members of the group is uncertain. Further he states that the Gasterostomidae by the structure of the cercaria as shown in the oral sucker and the presence and relations of the oral evaginations, doubtless belongs to the Paramphistomidae. His derivation of the gasterostomes thus from amphistome-like forms of frogs is plausible since the frogs serve as food for the hosts of the gasterostomes. To Odhner's argument may be added that the divided condition of the body in Gastrodiscus recalls the similar condition in certain Aspidogastridae and suggests a possible relationship between these forms. The morphological comparisons of Odhner and other writers appear to show very clearly that divergence and convergence have both had great influence on the phylogeny of certain trematode families.

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A preliminary description was given in the Journal of Parasitology, 3:21-27.

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EXPLANATION OF PLATES

All figures except those of reconstruction were drawn with the aid of a camera lucida and were made from permanent mounts.

Abbreviations used

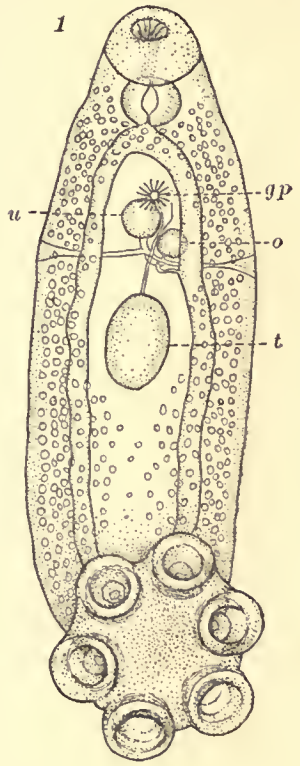
a	acetabulum	*nc*	nerve commissure
b	esophageal bulb	*o*	ovary
cm	circular muscles	*oc*	eye spot
cs	cirrus sac	*od*	oviduct
e	esophagus	*om*	oblique muscles
ed	excretory duct	*oo*	ootype
ep	excretory pore	*op*	oral evagination
gp	genital pore	*os*	oral sucker
gc	genito-intestinal canal	*ov*	egg
h	small hooklets	*p*	postate gland
hd	hermaphroditic duct	*ph*	pharynx
i	intestine	*sp*	septum
l	Laurer's canal	*sv*	seminal vesicle
lm	longitudinal muscles	*t*	testis
ls	lymph sinus	*u*	uterus
lt	limiting membrane	*ud*	uterine duct
m	mouth	*v*	vitellaria
md	median dorsal lymph canal	*vd*	vas deferens
mg	Mehlis' gland	*vg*	vagina
mo	marginal organ	*vl*	vitelline duct
mt	metraterm	*vv*	vitello-vaginal canal
mv	median ventral lymph canal		

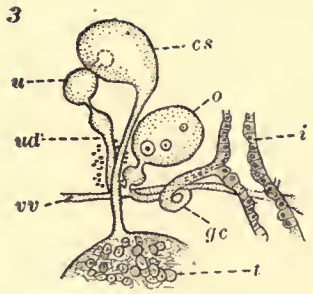
PLATE I

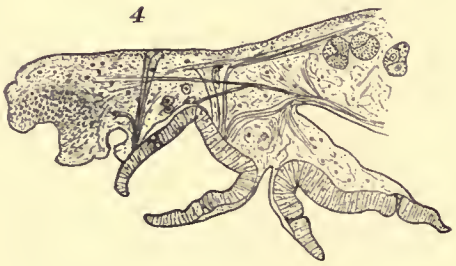
EXPLANATION OF PLATE

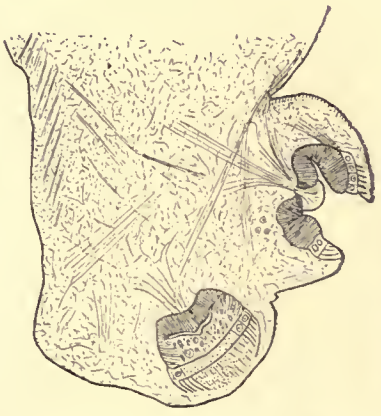
POLYSTOMA ORBICULARE

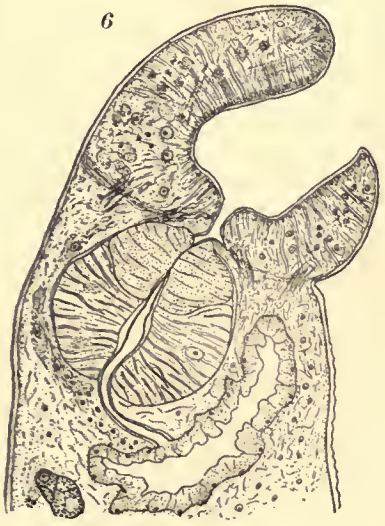
Fig. 1. Entire specimen, extended, ventral view. × 35.
Fig. 2. Hook from genital coronet. × 225.
Fig. 3. Reconstruction of genital apparatus from frontal sections. × 135.
Fig. 4. Sagittal section thru caudal disc. × 87.
Fig. 5. Frontal section thru caudal disc. × 73.
Fig. 6. Sagittal section thru oral sucker and pharynx. × 140.











STUNKARD NORTH AMERICAN POLYSTOMIDAE PLATE I

PLATE II

EXPLANATION OF PLATE

POLYSTOMA ORBICULARE

Fig. 7. Frontal section. × 35.

Fig. 8. Frontal section of ootype and beginning of uterine duct. × 185.

Fig. 9. Frontal section of ootype and end of right vitello-vaginal canal, five sections ventral to Figure 8. × 185.

Fig. 10. Frontal section, ootype region of same specimen as Figures 8 and 9, showing ovary, uterus, oviduct, uterine duct, genito-intestinal canal and vas deferens. × 140.

Fig. 11. Frontal section showing vitellaria and origin of vitelline ducts with granular secretion in the cells and duct. × 87.

Fig. 12. Frontal section thru cirrus sac at the juncture of the shanks and roots of the genital hooks, showing the genital papillae cut across, and a section of the duct from the uterus at the bottom of the figure. × 250.

Fig. 13. Reconstruction of male genital apparatus from sagittal sections. × 140.

Fig. 14. Frontal section thru uterus showing embryo in stage of a morula-like mass of cells. × 700.

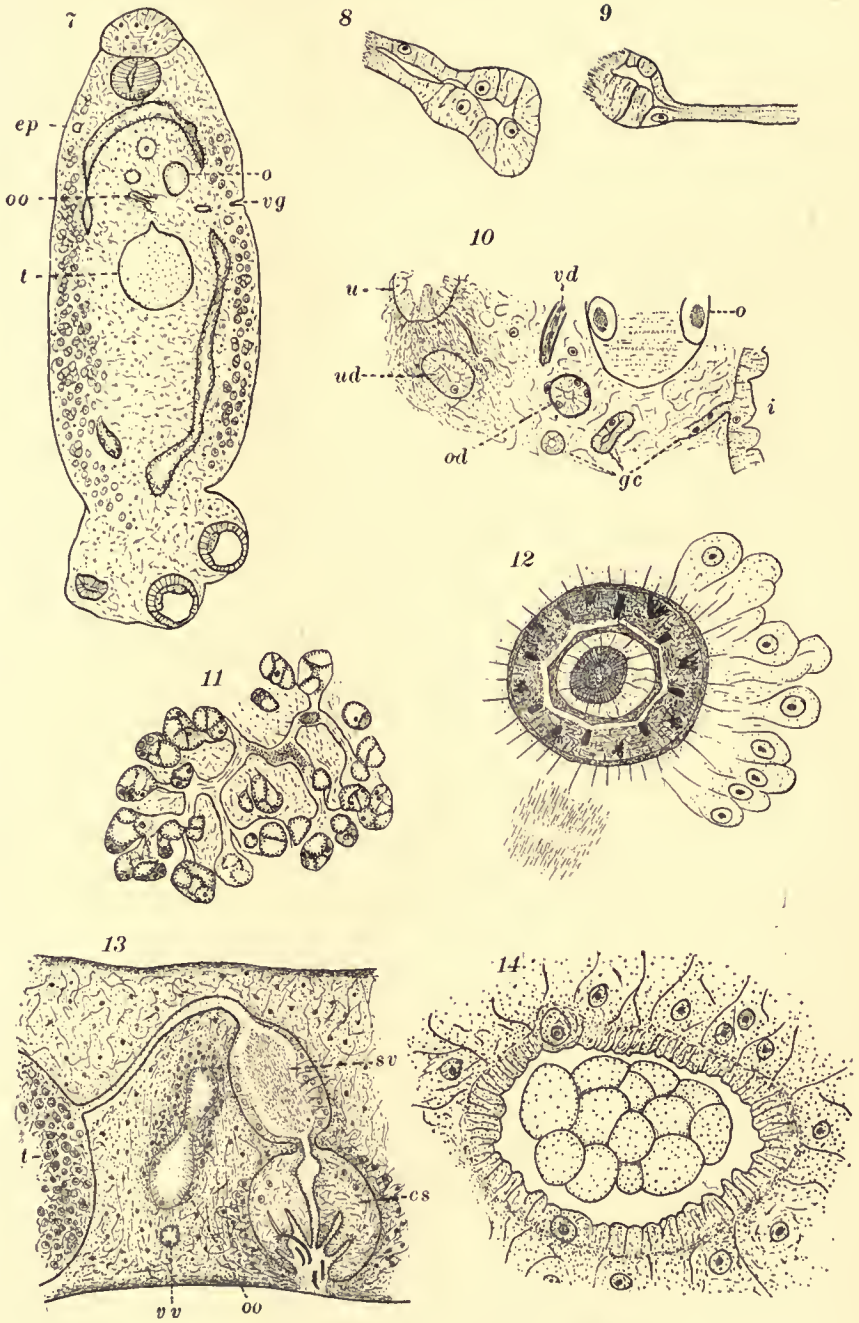

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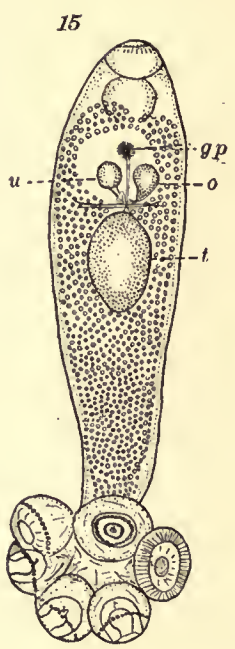
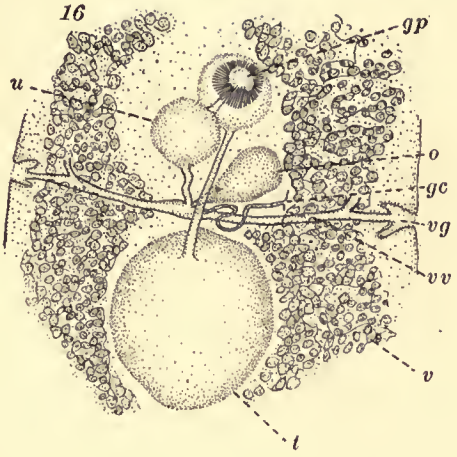
PLATE III

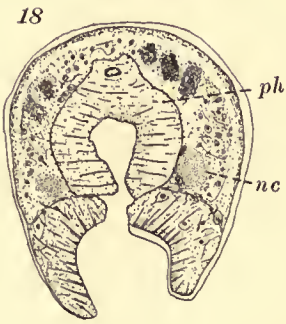
EXPLANATION OF PLATE

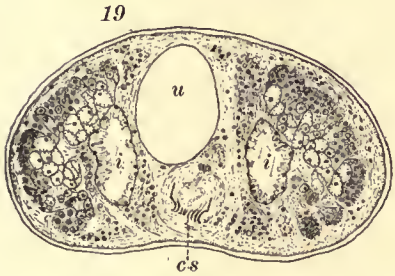
POLYSTOMA OPACUM

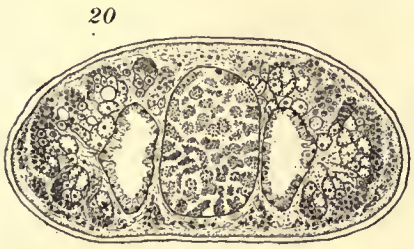
Fig. 15. Entire specimen, extended, ventral view. × 20.
Fig. 16. Reconstruction of genital apparatus from toto preparation and cross sections. × 50.
Fig. 17. Hook from genital coronet. × 550.
Fig. 18. Frontal section thru the anterior sucker and pharynx, showing in section nerve commissures and vitellaria. × 60.
Fig. 19. Cross section of body thru uterus and cirrus sac. × 60.
Fig. 20. Cross section of body thru the testis. × 60.
Fig. 21. Cross section thru the anterior pair of bothria. × 60.

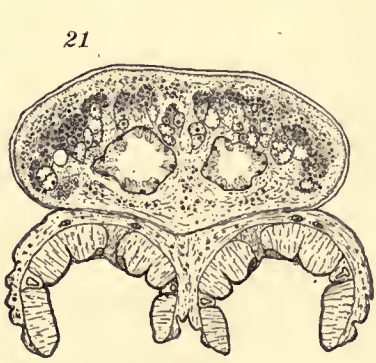












STUNKARD NORTH AMERICAN POLYSTOMIDAE PLATE III

PLATE IV

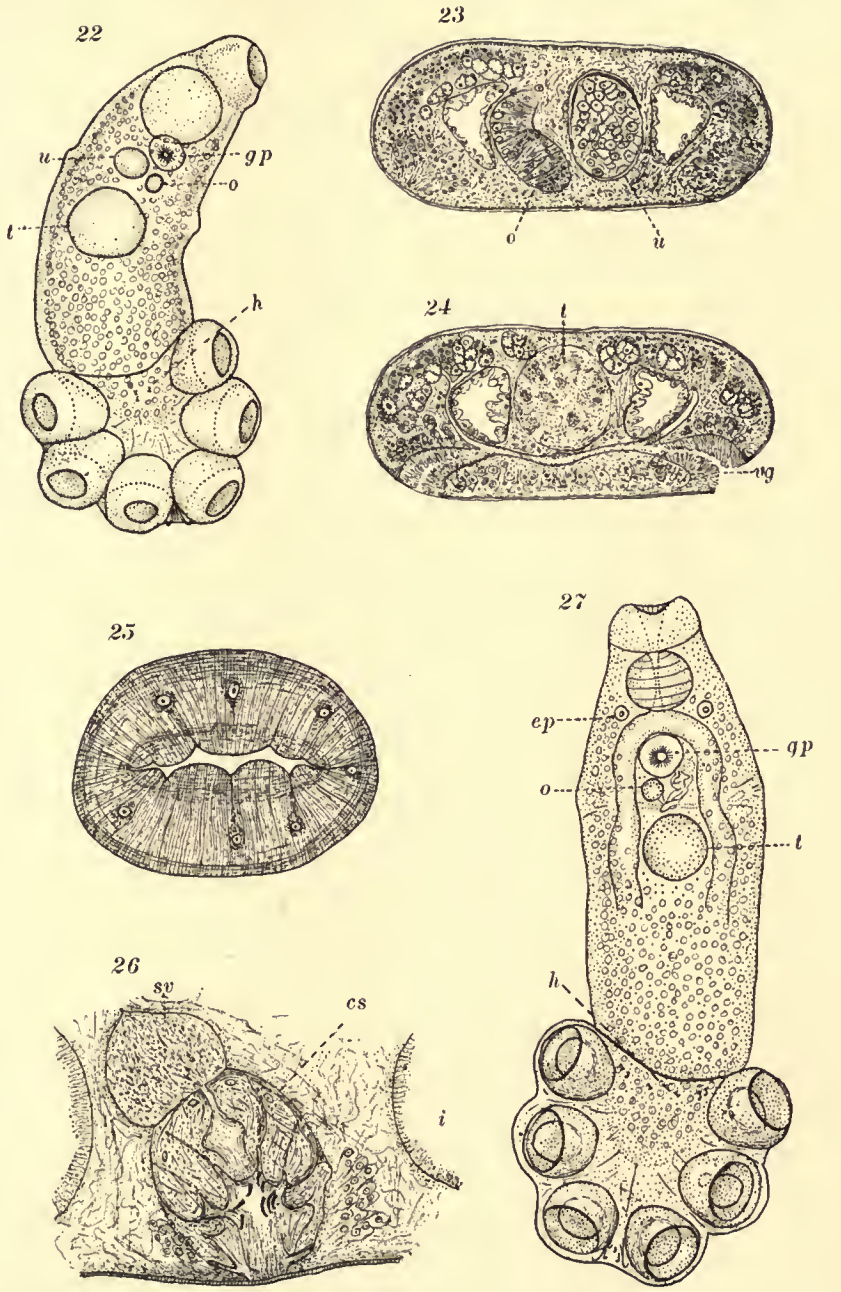
EXPLANATION OF PLATE

Polystoma megacotyle

Fig. 22. Entire specimen, ventral view. × 27.
Fig. 23. Cross section of body thru ovary and uterus. × 60.
Fig. 24. Cross section of body thru vaginae and anterior part of the testis. × 60.
Fig. 25. Cross section thru the pharynx near the posterior end. × 85.
Fig. 26. Cross section of seminal vesicle and cirrus sac. × 140.

Polystoma coronatum

Fig. 27. Entire specimen, ventral view. × 27.



STUNKARD NORTH AMERICAN POLYSTOMIDAE PLATE IV

PLATE V

EXPLANATION OF PLATE

POLYSTOMA MICROCOTYLE

Fig. 28. Entire specimen, ventral view. × 27.

Fig. 29. Ventral view of caudal disc, showing arrangement of musculature and hooks. × 43.

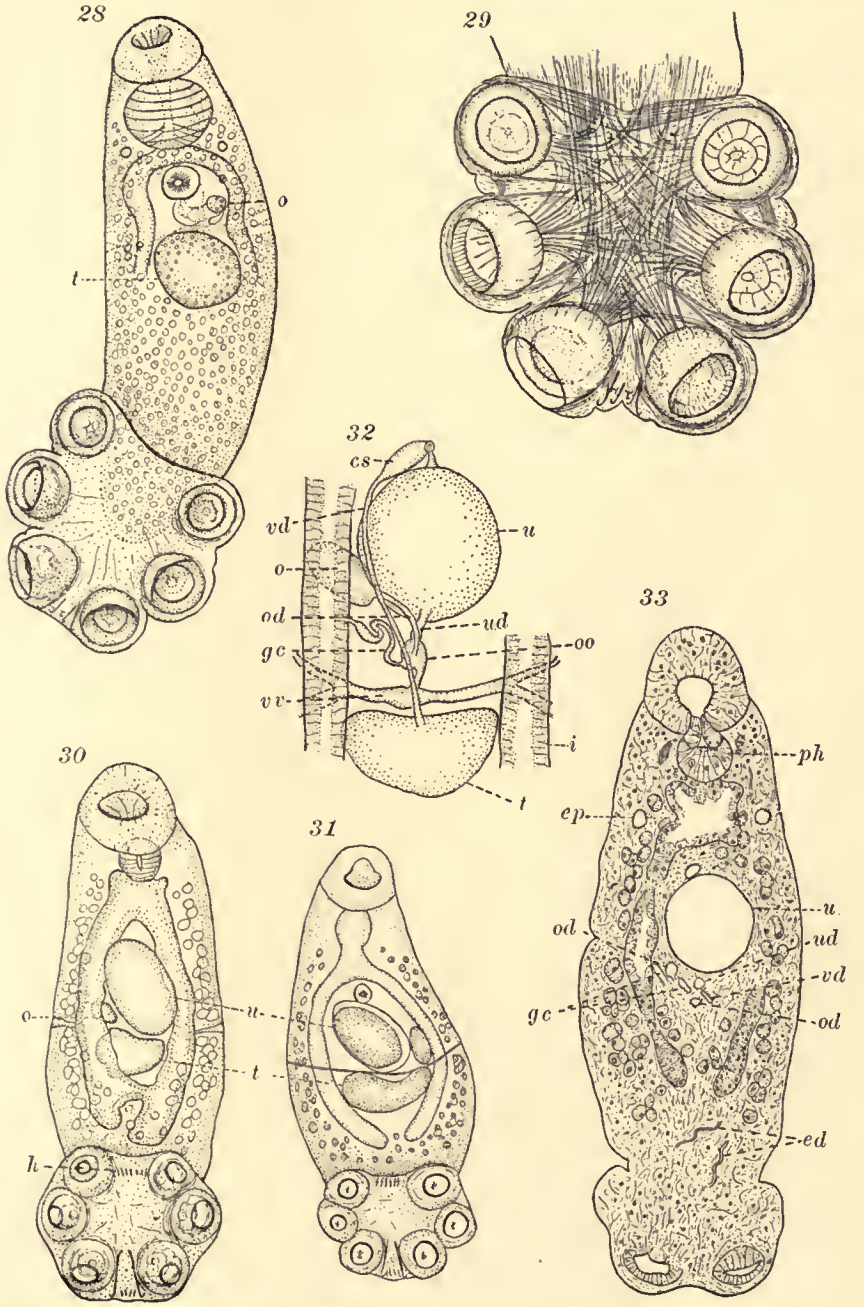
POLYSTOMA HASSALLI

Fig. 30. Entire specimen, ventral view, ceca connected posteriorly. × 45.

Fig. 31. Entire specimen, ventral view, in which there is no posterior connexion between the ceca. × 40.

Fig. 32. Reconstruction of genital apparatus from frontal sections. × 135.

Fig. 33. Frontal section thru the dorsal part of the uterus, showing oral sucker, pharynx, nerve commissures, intestine, excretory vesicles and ducts, vitellaria and smaller tubes of the ootype region. × 60.



STUNKARD NORTH AMERICAN POLYSTOMIDAE PLATE V

PLATE VI

EXPLANATION OF PLATE

SUCKERS AND HOOKS OF VARIOUS SPECIES OF POLYSTOMES

Fig. 34. *Polystoma orbiculare*, bothrium from caudal disc. × 140.
Fig. 35. *Polystoma orbiculare*, frontal section thru bothrium. × 140.
Fig. 36. *Polystoma obiculare*, optical section of bothrium showing cuticular framework. × 140.
Fig. 37. *Polystoma opacum*, hook from base of sucker. × 165.
Fig. 38. *Polystoma opacum*, hook from anterior margin of caudal disc. × 165.
Fig. 39. *Polystoma microcotyle*, hooks of posterior margin of disc. × 165.
Fig. 40. *Polystoma opacum*, hooks of posterior margin of disc. × 165.
Fig. 41. *Polystoma megacotyle*, hooks of posterior margin of disc. × 165.
Fig. 42. *Polystoma coronatum*, hooks of posterior margin of disc. × 165.
Fig. 43. *Polystoma orbiculare*, hook from base of sucker. × 165.
Fig. 44. *Polystoma orbiculare*, frontal section thru a sucker illustrating the method of operation; the external zones are retracted with the resulting protrusion of the basal part. × 140.
Fig. 45. *Polystoma integerrimum*, frontal section thru a sucker showing type of cuticular framework. Compare with text and types illustrated in other figures. × 100.

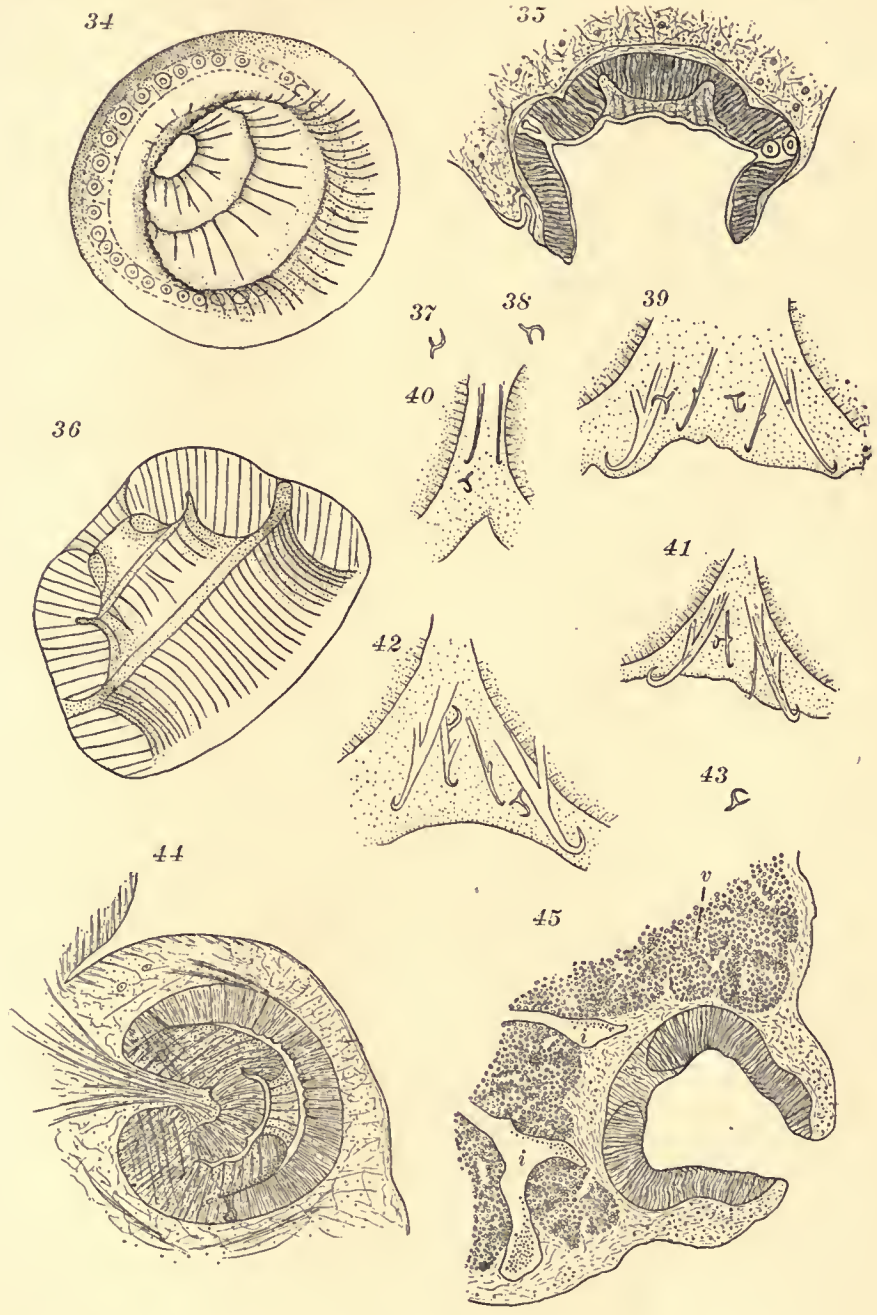

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PLATE VII

EXPLANATION OF PLATE

COTYLASPIS COKERI

Fig. 46. Entire specimen, extended, dorsal view. × 40.

Fig. 47. Ventral view of entire specimen showing position of marginal organs and divisions of the adhesive disc. × 40.

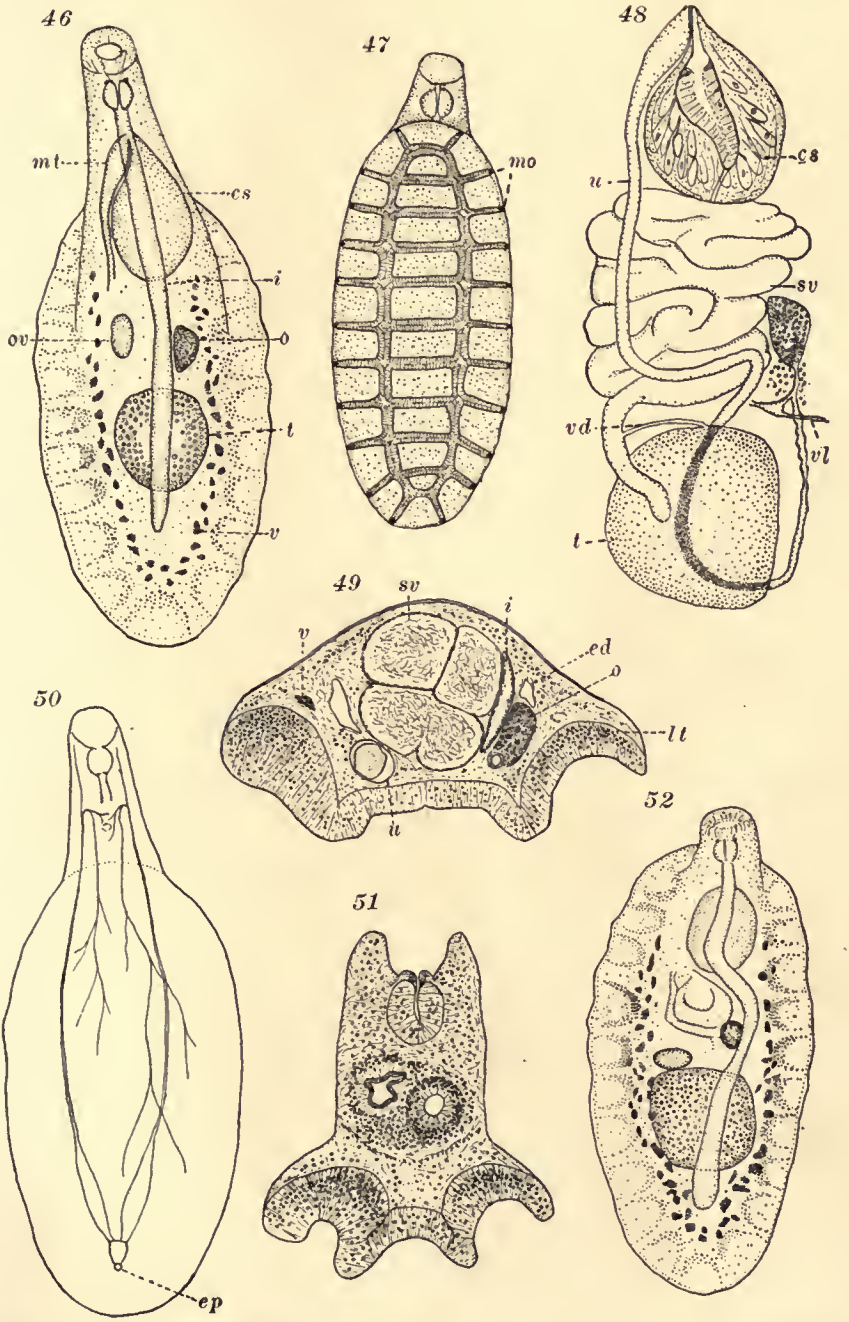
Fig. 48. Reconstruction of reproductive organs from frontal sections. × 80.

Fig. 49. Cross section of body at the level of the ovary showing the ovary, uterus, seminal vesicle, intestine, excretory ducts, and a follicle of the vitellaria. × 87.

Fig. 50. Diagrammatic representation of the excretory system from a living specimen, dorsal view. × 40.

Fig. 51. Oblique section of body just posterior to the genital pores, showing in section the mouth funnel, pharynx, cirrus sac, uterus, septum and adhesive disc. × 87.

Fig. 52. Entire specimen, contracted, dorsal view. × 40.



STUNKARD NORTH AMERICAN ASPIDOGASTRIDAE PLATE VII

PLATE VIII

EXPLANATION OF PLATE

COTYLASPIS COKERI (EXCEPT FIGURE 56)

Fig. 53. Sagittal section thru the anterior end of body showing musculature, digestive and reproductive organs. × 200.

Fig. 54. Frontal section thru the openings of the genital pores. × 85.

Fig. 55. Section thru a marginal organ; a muscle fiber is seen at the left of the figure and on the other side a nerve fibril passes to the inner end of the thick walled part of the canal. In this section the canal is cut across and can not be traced from the bulb to the exterior. × 580.

Fig. 56. Section thru a marginal organ in *Cotylaspis insignis*. × 580.

Fig. 57. Frontal section thru the adhesive disc showing arrangement of musculature. × 95.

Fig. 58. Section thru the anterior part of the forebody showing the base of the mouth funnel, anterior part of the pharynx, nerve commissure and eye spots. × 800.

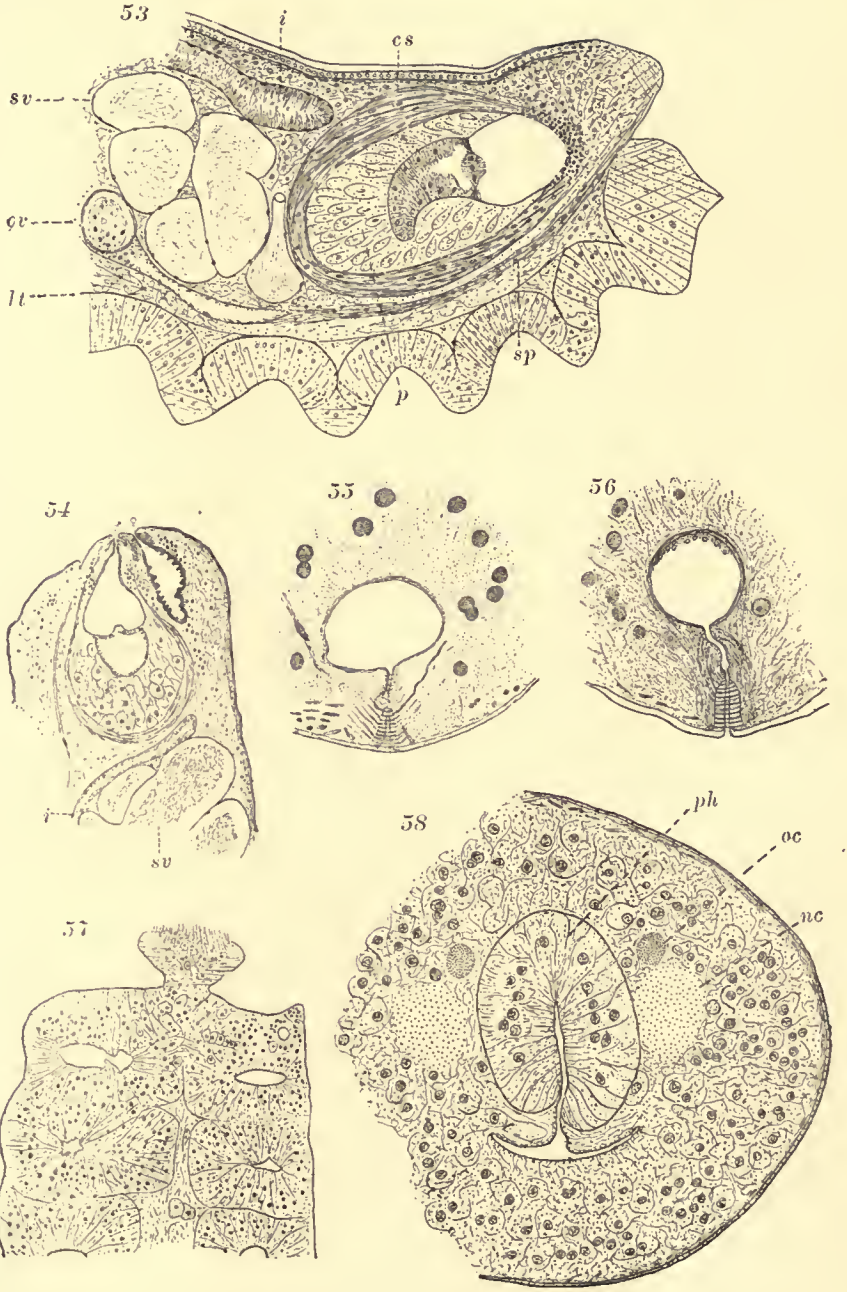

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PLATE IX

EXPLANATION OF PLATE

ALASSOSTOMA MAGNUM

Fig. 59. Entire specimen, ventral view. × 9.

Fig. 60. Cross section thru the genital pore showing the terminal parts of the cirrus sac and uterus, the hemaphroditic duct, genital sinus, four layers of muscles in the body wall and the muscle lamellae of the esophageal bulb. ×27.

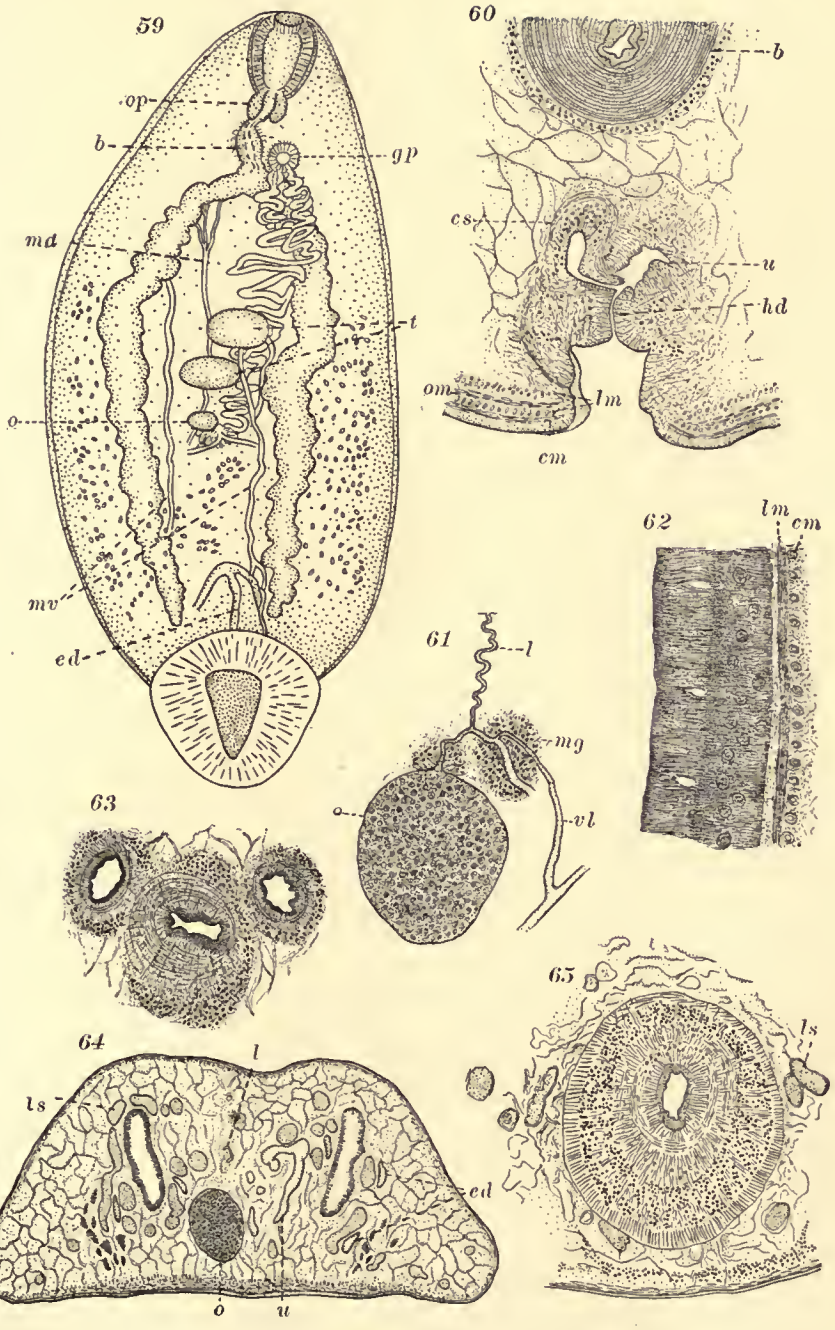
Fig. 61. Diagrammatic representation of female genital apparatus reconstructed from cross sections. ×40.

Fig. 62. Section of the wall of the intestine. ×360.

Fig. 63. Cross section thru the oral sucker and the oral evaginations. × 40.

Fig. 64. Cross section of body at the level of the ovary showing in section the ovary, uterus, Laurer's canal, the ceca, vitellaria, lymph spaces and excretory ducts. × 16.

Fig. 65. Cross section thru the oral sucker showing arrangement of muscle fibers and position of the nuclear zone. × 35.



STUNKARD NORTH AMERICAN PARAMPHISTOMIDAE PLATE IX

PLATE X

EXPLANATION OF PLATE

ALASSOSTOMA PARVUM

Fig. 66. Entire specimen, ventral view. × 27.

Fig. 67. Cross section of body posterior to the ovary showing coils of the excretory ducts. × 70.

Fig. 68. Cross section thru the posterior part of the acetabulum showing lymph spaces around the sucker. × 70.

Fig. 69. Cross section a short distance posterior to the genital pore showing in section, the uterus, the cirrus sac, and above the latter organ three loops of the seminal vesicle. × 70.

Fig. 70. Cross section of esophageal bulb with clusters of surrounding cells. × 70.

Fig. 71. Cross section of body thru the genital pore showing hermaphroditic duct, cirrus sac, lymph spaces and the character of the parenchyma. × 90.

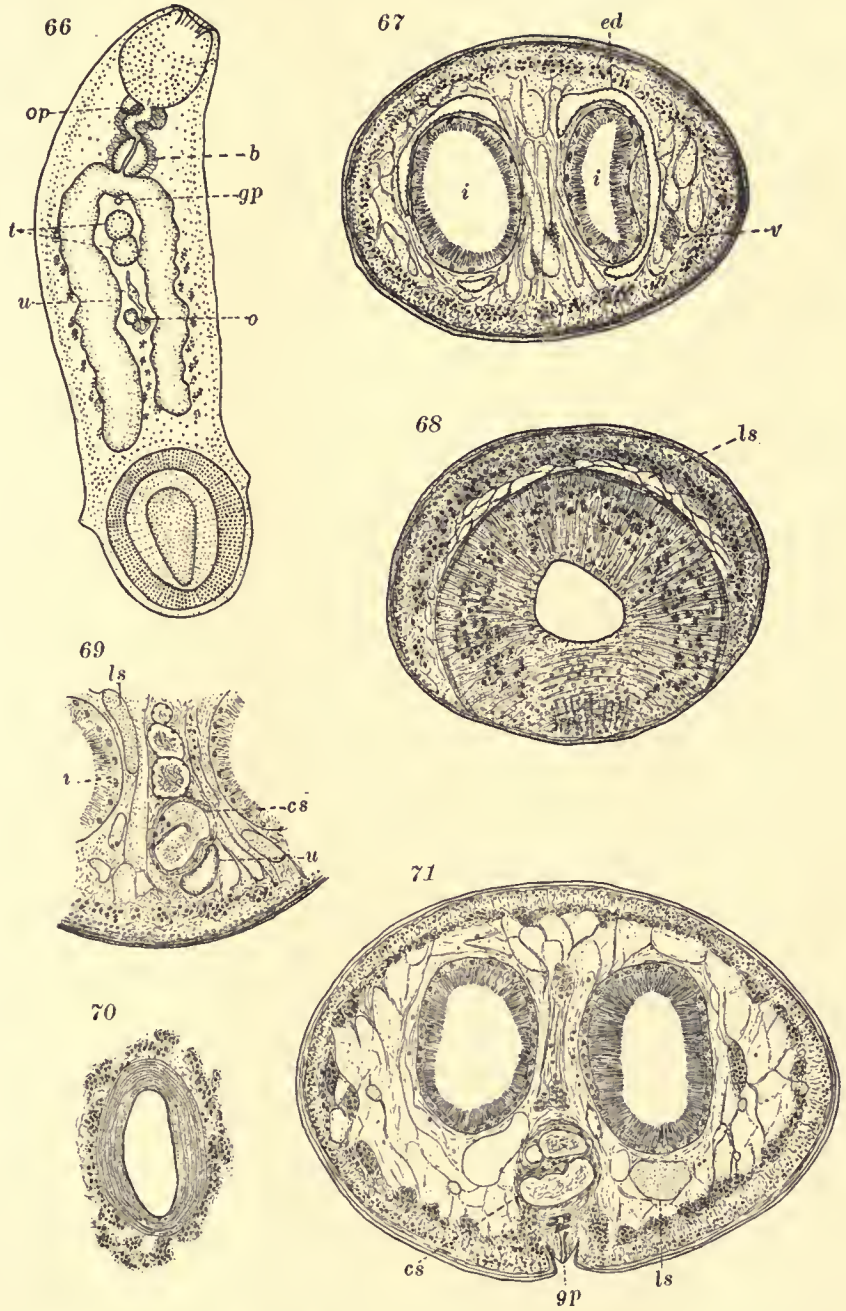

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PLATE XI

EXPLANATION OF PLATE

ZYGOCOTYLE CERATOSA

Fig. 72. Entire specimen, ventral view. × 11.

Fig. 73. Cross section of esophageal bulb, showing the arrangement of the muscle fibers. × 45. Compare with Figures 60 and 70.

Fig. 74. Cross section of body thru the origin of the oral evaginations. × 45.

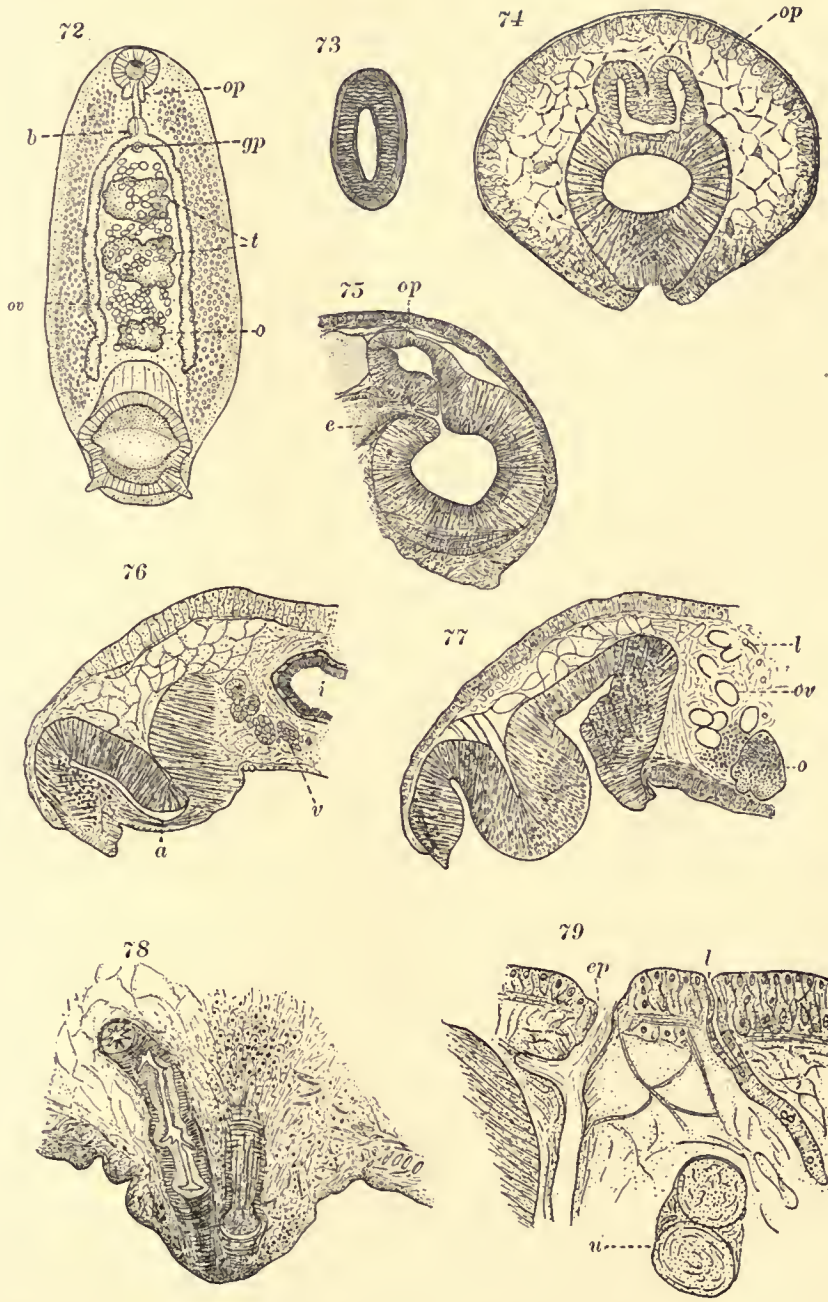
Fig. 75. Sagittal section thru the anterior part of the body showing oral sucker, an oral evagination and the anterior part of the esophagus. × 45.

Fig. 76. Sagittal section of posterior part of body thru one side of the acetabulum. × 27.

Fig. 77. Sagittal section of the posterior part of the body near the median line, showing the ovary, eggs in the uterus, Laurer's canal, and the shape of the acetabulum. × 27.

Fig. 78. Sagittal section thru the body one section at the side of the genital pores showing the folded wall of the uterus and the ejaculatory duct which in this species is without a cirrus sac. × 136.

Fig. 79. Representation of the sagittal section thru the openings of Laurer's canal and the excretory vesicle. × 90.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